Legacy of loss: seed dispersal by kererū and flightless birds in New Zealand

---

A thesis presented in partial fulfilment of the requirements for the degree of

Doctor of Philosophy

in

Ecology

at the University of Canterbury, Christchurch, New Zealand

Joanna K. Carpenter

2019

Abstract

The New Zealand avifauna has experienced dramatic losses since human arrival. I investigated how these declines and extinctions have affected seed dispersal. My first aim was to assess the current state of kererū (New Zealand pigeon, *Hemiphaga novaeseelandiae*) populations, by measuring trends in kererū detections and dispersal quantity of six plant species at Pelorus over three decades. Kererū detections declined significantly over the period, but there was no overall worsening in dispersal quantity. This is probably because kererū numbers did not change significantly during the autumn fruiting season, and other birds contributed to the dispersal of smaller-seeded species.

Secondly, I assessed whether the extinction of moa (Dinornithiformes), New Zealand's largest herbivores, created a 'gap' in the dispersal of large seeds. I compared the seed remains found in 152 moa coprolites and 23 subfossil moa gizzards. While large seeds were present in 48% of moa gizzards, the coprolites had an extremely finely ground consistency and contained no seeds larger than 3.3 mm. Since the powerful grinding in moa gizzards meant large seeds were predated, not dispersed, moa extinction has not reduced dispersal (except for some herbs and shrubs whose small seeds reached coprolites intact).

Thirdly, I investigated the role of an extant flightless bird, the weka (*Gallirallus australis*), in the dispersal of hīnau (*Elaeocarpus dentatus*). I measured hīnau dispersal from the canopy and the ground at two mainland New Zealand sites and two island bird sanctuary sites. I found that canopy fruit handling rates were low even on islands, which suggests that hīnau may be adapted for ground-based dispersal by flightless birds. Ground-based dispersal of hīnau was low on the mainland (4% seeds dispersed) compared to islands (76% dispersed), due to low frugivore numbers on the mainland. Weka conducted the majority of dispersal on islands.

Fourthly, I assessed the seed dispersal effectiveness of weka. I estimated the seed retention times of weka for hīnau and miro (*Prumnopitys ferruginea*), using PIT-tagged seeds. Weka had the longest avian seed retention times ever recorded (means of 38.5 hours for miro and 125.2 for hīnau). I obtained high-resolution weka movement data by GPS tagging 39 birds over three sites, then combined movement and seed retention time data in a mechanistic model to assess how far weka disperse hīnau and miro seeds. Weka

dispersed 93-97% of seeds away from the parent canopy, with 1% of seeds dispersed >1 km.

My findings demonstrate that unexpected bird species are providing important seed dispersal services, and that New Zealand seed dispersal networks may therefore be less resilient to frugivore loss than they initially appear. Fortunately, the key flightless avian disperser identified in my results is still extant, meaning that restoration of this ecosystem service is possible.

Acknowledgements

This PhD has taken me up hill and down dale, from the sunny climes of Kapiti Island to the stormy squalls of Foveaux Strait. Very little of it would have been possible without the support of an amazing crew of people. Like Isaac Newton, I have looked further by standing on the shoulders of giants. These are (some of) the giants.

First off, I am incredibly grateful to my primary supervisor Dave Kelly. Dave, thanks for putting up with me running away (temporarily) to join the kākāpō team, my addiction to the word 'critical', and my love of pictures on graphs. I always enjoyed our wide-ranging ecology chats over flat whites at Café 101, and your enthusiasm for all the weird and wonderful things I found out over the course of this PhD. I couldn't have asked for a better supervisor. Thanks also to my co-supervisors, Colin O'Donnell and Jim Briskie. Colin, thanks for your support, encouragement, late night whiskeys, and loan of DOC gear. Jim, you always provided helpful feedback whenever my supervisory panel meetings rolled around, and your insider knowledge of the Animal Ethics approval process made it far easier when I was trying to obtain permission to do weird things to birds.

Thanks also to Janet Wilmshurst and Jamie Wood, for listening to my erroneous hypotheses about moa as seed dispersers and then helping me turn those into an awesome paper. Janet, you've been a real source of inspiration for me and I love our enthusiastic discussions about rats, seeds, and everything in between. Mick Clout, BJ Karl, and Jenny Ladley were also kind enough to let me use valuable long-term datasets they had collected, which are normally far beyond the scope of a 3 year PhD. I'm also very grateful to Elena Moltchanova, for helping me with analysis and R code.

Many wonderful people helped out with my fieldwork. Special thanks must go to Kim Roberts, for organising things on campus for me when I was far away, planting out seeds with me, and keeping me company while scrounging in the dirt looking for defecated weka seeds at Willowbank. Jo Ledington, Archie MacFarlane, Lyndsay Murray, Kirsten Rodgers, Helen Armstrong, Ellen Irwin, Jane Furkett, Theo Thompson, Blair Sandford, Robyn White, Siobain Browning, Robyn Long, Amira Perry, Leighton

Thomas all laboured in the field with me in good weather and bad, peering at seeds or wrangling weka. You are all absolute champions and I couldn't have done this without you. Jo Monks, Jim Watts, Nyil Khwaja, Jo Ledington, and Jamie McAulay all provided advice, inspiration, and a kind ear (or package of mist nets in Jamie's case) at times of desperation. Jim in particular was my ArcGIS guru and any beautiful maps in this thesis must first and foremost be attributed to his skills.

The support I received from DOC staff at Hokitika, Rakiura, Picton, and Kenepuru was humbling. Aubrey Tai, Joe Healey, Nick Fisentzidis, Gen Spargo, and Antje Whalberg in particular went the extra mile and made all my fieldwork so much easier. Stu Cockburn provided me with much needed technical expertise for my RFID research – thanks so much Stu. Paul van Klink and Joris Tinnemans kindly trained me in the vagaries of weka capture. The staff at Willowbank Wildlife Reserve also deserve a special mention for being so accommodating while I lugged 12V batteries around and set up ugly scanning devices in their weka enclosures.

I was lucky enough to be the recipient of several grants over the course of this PhD, without which this work would not have been possible. Thank you to the Auckland Botanical Society, Koiata Trust, Birds NZ, Brian Mason Scientific and Technical Trust, Graduate Women of New Zealand, and New Zealand Ecological Society for supporting my research. I am also grateful to UC for awarding me with a Roper Scholarship in Science.

Lastly, thank you to my parents and my partner Theo. Theo, your unwavering support, problem-solving brain, and practical talents made many of the problems I faced during my PhD far less daunting. Thank you for always having faith in my abilities, and buying me a heat gun when you saw I needed one. My parents have always fostered in me a love of nature, which has been the keystone to my fledgling career in ecology. Thanks to them I have grown from an undergraduate seed to a PhD sapling. Mum, Dad, and Collie - I am so grateful for your support, belief, and love.

Declaration of Contributions

Chapter 2: Trends in the detections of a large frugivore (*Hemiphaga novaeseelandiae*) and fleshy-fruited seed dispersal over three decades

Main author: Jo Carpenter

Contributors: Dave Kelly, BJ Karl, Mick Clout, Jenny Ladley

JC formulated hypotheses, analysed the data, and wrote the manuscript. BJK, MC, DK, and JL collected the data, and made comments on the draft manuscript. DK created Figure 2.2.

Chapter 3: An avian seed dispersal paradox: New Zealand's extinct megafaunal birds did not disperse large seeds

Main author: Jo Carpenter

Contributors: Dave Kelly, Janet M Wilmshurst, Jamie Wood

JC and JMW formulated hypotheses. JW collated the moa coprolite/gizzard dataset. DK collected the germination data. JC analysed the data and wrote the manuscript. DK, JW, and JMW made comments on the draft manuscript.

Chapter 4: Introduction of mammalian seed predators and the loss of an endemic flightless bird impair seed dispersal of the New Zealand tree *Elaeocarpus dentatus*

Main author: Jo Carpenter

Contributors: Dave Kelly, Colin O'Donnell, Elena Moltchanova

JC formulated hypotheses, designed the study, collected the data, analysed the data (except for the Bayesian analysis, which was performed by EM), and wrote the manuscript. DK, COD, and EM made comments on the draft MS.

Chapter 5: Passive integrated transponder (PIT) tagged seeds reveal extremely long seed retention times in a flightless rail (*Gallirallus australis*)

Main author: Jo Carpenter

Contributors: Dave Kelly

JC formulated hypotheses, designed the study, collected the data, analysed the data, and wrote the manuscript. DK assisted with data collection and made comments on the draft manuscript.

Chapter 6: Long seed dispersal distances by an inquisitive flightless rail (*Gallirallus australis*) are reduced by interaction with humans.

Main author: Jo Carpenter

Contributors: Dave Kelly, Colin O'Donnell, Elena Moltchanova

JC formulated hypotheses, designed the study, collected the data, and wrote the manuscript. EM wrote the R code to perform the mechanistic model and JC performed all other analyses. DK, COD, and EM made comments on the draft manuscript.

Table of Contents

1

Introduction to seed dispersal

Kererū consuming karaka (*Corynocarpus laevigatus) fruits.*
Credit: Manaaki Barrett

1.1 What is seed dispersal?

Seed dispersal is a vital ecosystem process which influences plant survival, patterns of plant establishment (Godinez-Alvarez et al. 2009), community dynamics (Levine and Murrell 2003) and species richness (Howe and Smallwood 1982; Wandrag et al. 2017). It can be defined simply as the movement of seeds away from the maternal parent (the 'parent plant') which produced them. This movement can be facilitated by abiotic factors (wind, gravity, or water), or biotic agents (animals). Plants with animal-mediated seed dispersal constitute 64% and 27% of gymnosperm and angiosperm lineages respectively (Herrera and Pellmyr 2009), suggesting the high adaptive value of biotic seed dispersal for sessile plants.

Biotic agents can disperse seeds either internally, by consuming the seed and regurgitating or defecating it later (endozoochory), or externally, by the seed attaching to the exterior of the animal and later dislodging (epizoochory). Certain rodents and birds disperse seeds as a by-product of seed predation by creating caches of seeds (also known as scatter hoarding), some of which are not eaten and therefore manage to germinate (e.g. Vander Wall 2001; Hirsch et al. 2012). This dispersal mechanism is associated with significant seed mortality, as the rodents function primarily as seed predators (antagonists) rather than dispersers (mutualists).

Endozoochory is generally a mutualistic interaction, where seeds provide a nutritious reward for the animal disperser in the form of fleshy appendages or coverings. Birds and mammals are the most common endozoochorous seed dispersers (Howe 1986; Stiles 2000), but tortoises (Jerozolimski et al. 2009; Blake et al. 2012), lizards (Olesen and Valido 2003; Wotton et al. 2016), fish (Galetti et al. 2008; Correa et al. 2016) and perhaps even invertebrates (Duthie et al. 2006; De Vega et al. 2011; but see Wyman et al. 2011) also perform important seed dispersal services in some systems.

The potential benefits to plants of animal-mediated seed dispersal are (1) escape from density-dependent seed mortality (the escape hypothesis), (2) colonization of rare, unpredictable sites (colonization hypothesis), (3) directed dispersal to ideal microsites (directed dispersal hypothesis), and (4) improved germination through gut passage

(Howe and Smallwood 1982; Traveset and Verdú 2002). Long-distance dispersal events also have important implications for plant population spread and the maintenance of genetic connectivity, especially in fragmented forests (Trakhtenbrot et al. 2005). As dispersal is frequently a complex, multi-stage process, these benefits are not mutually exclusive, and often work synergistically.

Benefit (1): The escape hypothesis, often called the Janzen-Connell hypothesis as it was first proposed independently by Janzen (1970) and Connell (1971), predicts that seedlings will suffer from high mortality under parent trees due to host-specific seed predators, pathogen attacks, and/or seedling competition (Howe and Smallwood 1982). These factors work in a density- or distance- dependent fashion so that seedling mortality reduces as distance from the parent tree increases or local density decreases (Wenny 2001), thereby making dispersal advantageous. For example, Janzen et al. (1976) found that bat-dispersed *Andira inermis* seeds were killed in a distance- and density- dependent fashion by *Cleogonus* weevils, resulting in seeds having 60% mortality under parent trees, 30% mortality under feeding roosts, and 10% mortality when dispersed between parent trees and feeding roosts. A recent meta-analysis found significant support for the Janzen-Connell hypothesis's density- and distance-dependent predictions regarding propagule survival (Comita et al. 2014). Across all studies combined, survival rates were significantly reduced near conspecifics compared to far from conspecifics, and in areas with high densities of conspecifics compared to areas with low conspecific densities. Effects were significantly stronger in the seedling stage compared to the seed stage, and there was a trend for stronger distance and density dependence at sites with higher, rather than lower, annual precipitation. Aside from providing selective benefits to the plants whose seeds are dispersed, Janzen-Connell effects promote species co-existence and maintain diversity of plant communities.

Benefit (2): Seed dispersal is also helpful for the colonisation of new unoccupied habitat, especially ephemeral habitats that are unpredictable in space or time, such as treefall gaps. For species that rely on such microsites, a widespread dispersal shadow - the spatial distribution of seeds from one parent plant - increases the probability of

some seeds being in the right place for a suitable microsite occurring later in time, or for arriving shortly after the suitable habitat is created (Wenny 2001).

Benefit (3): Directed dispersal occurs when dispersal agents disproportionately move seeds to favourable sites conducive to higher seedling survival (Wenny 2001). For example, in Israel Yellow-vented Bulbuls (*Pycnonotus xanthopygos)* consume mistletoe (*Plicosepalus acaciae)* fruits and defecate the viscous seeds on to *Acacia raddiana* and *A. tortilis*, the mistletoe's host trees (Green et al. 2009). Similarly, while introduced mammals in the New Zealand alpine zone consume and disperse the seeds of several native plant species, only the native parrot kea (*Nestor notabilis*) move most of the seeds they handle to suitable microsites on distant mountain ranges (Young et al. 2012). It is controversial how common directed dispersal is, as animals move many seeds to unfavourable sites such as sleeping areas or beneath other conspecific trees, which can result in clumped seed deposition and lower recruitment (Kwit et al. 2007). However, Wenny (2001) argues that the research bias towards measuring the distance of seeds from the parent plant as opposed to microsite suitability has obscured the prevalence of directed dispersal.

Lastly, benefit (4): Ingestion by frugivores can increase the germination percentage (germinability) and rate (speed) of seeds (Traveset and Verdú 2002). This can occur through three different mechanisms: a) through the mechanical or chemical scarification of the seed coat (the 'scarification effect'); b) by the separation of seeds from the fruit pulp, which may contain inhibitory factors (the 'deinhibition effect'); and c) by the deposition of faecal material with the seed, which may have a positive influence on growth (the 'fertilization effect') (Traveset and Verdú 2002). Evidence for the fertilization effect is scarce, with the few studies variously showing faecal material having both positive and negative effects on germination (Cosyns et al. 2005; Tjelele et al. 2015). Conversely, the scarification effect has received a lot of attention in the literature, although its effect is typically small and inconsistent (Traveset 1998; Robertson et al. 2006; Traveset et al. 2007). The effect of scarification depends on disperser identity, the length of time that the seed remains in the gut passage, and the type of food ingested along with the seeds (Traveset et al. 2007). A literature review found that scarification effects (germination of hand-cleaned seeds compared to bird

ingested seeds) are significantly smaller than the less-often researched deinhibition effect (germination of hand-cleaned seeds compared to whole seeds) (Robertson et al. 2006). Considering that dispersal failure generally results in whole fruits falling undispersed to the ground beneath the parent tree, comparisons between whole fruits and hand-cleaned seeds are likely to be far more relevant when assessing the consequences of undispersed seeds.

For all the above reasons, dispersal provides benefits to plants by increasing seeds' survival prospects, consistent with the observation that so many lineages have evolved to offer rewards to biotic dispersers. That leads to an obvious question: what happens if the biotic dispersers disappear?

1.2 Effects of avian frugivore loss on seed dispersal

Seed dispersal systems are typically thought to be reasonably resilient to the loss of individual frugivores due to the systems' diffuse structure and lack of obligate partnerships (e.g. Timóteo et al. 2016). Generally, a seed dispersal network is comprised of each frugivore interacting with several plant species and each plant species being fed on by multiple frugivores (Yoshikawa and Isagi 2012). Therefore, other functionally similar frugivores may compensate for the loss of one seed disperser. For example, Timóteo et al. (2016) demonstrated that a Mediterranean seed dispersal network was resilient to the loss of the most abundant seed dispersing ant species, as the remaining ant species 'rewired' the network by widening their dietary breadth in a way that maintained seed dispersal services. Network theory describes such interactions as having high levels of redundancy, which results in communities that are more likely to persist in the face of extinctions (Mello et al. 2011). However, the species richness of a frugivore assemblage also has a significant effect on the *quality* of seed dispersal services, suggesting that maintaining the entire suite of frugivores may be more important than previously thought (Garcia and Martinez 2012). Dispersal quality refers to where the seed is deposited and the treatment of seeds within a frugivore's mouth or gut, whilst dispersal quantity encompasses visitation rates to fruiting trees and the number of seeds that are dispersed per visit (Schupp et al. 2010). While frugivores may exhibit functional similarity in their diets

(e.g. frugivore A and B each eat the same plant species), species-specific variation in seed dispersal quality and quantity is likely to be large (e.g. frugivore A eats few seeds, primarily disperses seeds beneath conspecific trees, and reduces germinability, while frugivore B consumes many seeds, disperses seeds to ideal microsites, and does not decrease germinability) (Jordano et al. 2007). Network theory often assumes that all dispersers offer the same service to the plants they disperse, ignoring differences in dispersal quality (but see Fricke et al. 2018).

Habitat loss, illegal harvesting, and depredation by invasive predators have resulted in global declines of frugivores, especially the larger-bodied ones, generating concern for seed dispersal networks despite the networks' apparently robust nature (Sekercioglu et al. 2004). Large-bodied frugivores are particularly susceptible to decline, due to their typically lower population densities, larger home ranges, and lower reproductive rates (Boyer 2010). The disproportionate loss of large-bodied frugivores often results in a 'downsizing' of the frugivore community, where the mean size of the frugivore assemblage decreases following human impacts. For example, Heinen et al. (2018) demonstrated that frugivore communities on oceanic islands have suffered from a strong extinction-driven decrease in mean body mass (mean downsizing 34%), with worrying ramifications for seed dispersal services. In addition, many ecosystems are already suffering from low diversity following hundreds of years of human impacts, which further exacerbates the effects of more recent frugivore declines (Corlett 2007; O'Farrill et al. 2013). In some cases frugivore losses have been so comprehensive that they have left plants relying on only one disperser, a potentially precarious situation (Rodríguez-Pérez and Traveset 2010). For example, the South American mistletoe *Tristerix corymbosus* suffered from recruitment failure when its sole disperser, the marsupial *Dromiciops gliroides*, became locally extinct (Rodríguez-Cabal et al. 2007).

Evidence is mounting that seed dispersal networks are suffering from the chronic loss of seed dispersers. McConkey et al. (2012) warned of a "growing, global seed dispersal crisis, which has so far been masked by the long lifespan of perennial plants". Frugivore declines have resulted in decreased fruit removal rates, affecting plant recruitment and eventually leading to possible population decreases for animal dispersed species (Brodie et al. 2009). Dry forests in Hawai'i have completely lost their

frugivore assemblage, and are now occupied by introduced birds which primarily disperse exotic plant species, resulting in most of the native trees' fruits falling undispersed beneath the parent trees (Chimera and Drake 2010; Pejchar 2015). Increasingly, studies are demonstrating shifts in tree species composition towards smaller-seeded or wind dispersed species in forests where frugivores have been lost (Cordeiro and Howe 2001; Terborgh et al. 2008; Vanthomme et al. 2010).

Demonstrating convincing demographic consequences of dispersal failure is difficult due to the long life span of most tree species, and because seed dispersal has low impact on population dynamics (low elasticity) relative to other factors affecting vital rates (Brodie et al. 2009). However, several studies have demonstrated impaired recruitment where animal-dispersed plants have lost their mutualistic partners. In the Canarian archipelago, populations of *Neochamaelea pulverulenta* on islands that have lost the largest frugivorous lizard species have reduced seedling recruitment outside the canopy and reduced effective recruitment rate, despite small and medium sized lizard dispersers still being present (Pérez-Méndez et al. 2015). The plant populations on these islands also have higher genetic similarity and smaller effective population sizes compared to populations where large frugivorous lizards remain (Pérez-Méndez et al. 2016). In Guam, predation by the invasive snake *Boiga irregularis* has resulted in the local extinction of most frugivorous bird species, resulting in a 61-92% decline in seedling recruitment for two tree species (Rogers et al. 2017), and the decline of a socially valued bird-dispersed plant, *Capsicum frutescens* (Egerer et al. 2018). In addition, the absence of frugivorous birds in Guam has led to an absence of seed rain in degraded forests, suggesting that these forests will suffer from delayed regeneration compared to frugivore-rich degraded forests in nearby Saipan (Caves et al. 2013). Finally, Christian (2001) demonstrated that the invasion of South African shrub lands by the invasive Argentine ant disrupted seed dispersal services and led to a shift in the composition of the plant community, due to a disproportionate reduction in the densities of large-seeded plants.

1.3 Seed dispersal in New Zealand

Biotic seed dispersal is a vital process in New Zealand's forests, with over 59% of trees and 48% of all woody plants producing fruits that are dispersed by frugivores (Burrows 1994; Kelly et al. 2010). New Zealand's 80 million year isolation from other landmasses has created an unusual suite of frugivores, dominated by birds and almost entirely devoid of mammals. Lizards, weta, and one species of bat are the only native non-avian dispersers. Lizards may be important dispersers of divaricating shrubs, especially in scrublands lacking frugivorous birds (Wotton et al. 2016), while the New Zealand lesser short-tailed bat (*Mystacina tuberculata*) disperses the fruits of several plants, including kiekie (*Freycinetia banksii*) and two species of *Collospermum* (Daniel 1976; Lord 1991). Weta have been shown to move some seeds small distances, although they also destroy many seeds and hence their contribution is probably negligible or even a net negative (Duthie et al. 2006; Wyman et al. 2011). Therefore birds, both flightless and volant, conduct the majority of New Zealand's biotic seed dispersal.

The arrival of humans in ca. 1280 C.E. (Wilmshurst et al. 2008) brought about substantial changes for the New Zealand biota, especially due to habitat clearance and the introduction of mammalian predators. The Polynesian rat (*Rattus exulans*) was introduced in the 13th century C.E. (Wilmshurst and Higham 2004), followed by Norway rats (*Rattus norvegicus*) in 1769 and ship rats (*Rattus rattus*) in the second half of the 19th century (Towns and Broome 2003). Stoats (*Mustela erminea*), weasels (*M. nivalis*), ferrets (*M. furo*), cats (*Felis catus*), mice (*Mus musculus*) and possums (*Trichosurus vulpecula*) were also introduced, to devastating effect. These immigrants affected seed dispersal both indirectly, by heavily predating frugivore populations (sometimes to local or global extinction), and directly through seed predation. Thorsen et al. (2011) estimated that the country has lost 57% of volant frugivores and 80% of flightless frugivores since human arrival. Huia (*Heteralocha acutirostris*) and piopio (*Turnagra capensis*) both consumed fruits and are now extinct (Clout and Hay 1989). Additionally, tīeke (saddleback; *Philesturnus spp.*) and kōkako (*Callaeus cinerea*) are important frugivores that are now so severely range-restricted that they can be considered functionally extinct. Species that are endangered, critically endangered, or

extinct in the wild can be classified as functionally extinct where they are locally absent or present at densities too low to be useful to plants (Sekercioglu et al. 2004). Currently, 84% of avian seed dispersal services are performed by only four species: endemic kererū (*Hemiphaga novaeseelandiae*), bellbirds (*Anthornis melanura*), tūī (*Prosthemadera novaeseelandiae*), and native (but recently arrived) silvereyes (*Zosterops lateralis*) (Kelly et al. 2006).

Although the important volant dispersers may remain, almost an entire suite of flightless presumed avian frugivores has been extirpated, including nine species of moa (Perry et al. 2014), and the role that these species played in seed dispersal is still unclear. Ground collection of fruit by moa is likely to have been an important dispersal mechanism for many plant species, especially those with large seeds (Lee et al. 1991; Forsyth et al. 2010). If no functional analogues remain, then plants that were primarily dispersed by moa historically may be currently experiencing low dispersal rates and possible dispersal failure. Moa are related to the cassowary (*Casuarius spp.*), a prolific and important disperser which picks fruits off the ground and moves them away from parent trees (Bradford et al. 2008). Moa gizzards found in North Canterbury and coprolites found in Central Otago contained an abundance of seeds, suggesting that fruit may have been an important part of their diet (Wood et al. 2008). Since moa became extinct in the 15th century (Perry et al. 2014), however, it is difficult to now evaluate how significant their seed dispersal contributions were. The existence of unusual apparently moa-adapted seeds would be highly suggestive, but evidence for such anachronisms is limited (Lord 2002; Thorsen et al. 2011), although Kelly et al. (2010) suggest that several large-seeded plant species with very slow germination may be adapted for moa dispersal. Lord (2002) speculated that seeds that were adapted for moa dispersal should fall to the ground when ripe, be conspicuous on the forest floor, and have a thick endocarp that could withstand the considerable grinding of a moa gizzard (which could contain up to 5kg of gizzard stones; Lee et al. 1991). Lee et al. (1991) also suggested that the large seed load of moa would have resulted in clumps of seeds being deposited, requiring plant species to be strongly shade-tolerant, and resistant to insects, herbivores, pathogens and seedling competition. One tree species that meets these criteria is hīnau (*Elaeocarpus dentatus*), a lowland forest tree with

large, shiny fruits that feature a very thick endocarp and drop to the ground when ripe (Lord 2002). The only extant frugivores recorded consuming hīnau fruits are kererū, kōkako, weka (*Gallirallus australis*), and brown kiwi (*Apteryx mantelli*) (Clout and Hay 1989; Kelly et al. 2010), three of which are severely range restricted. Consequently, hīnau could be suffering from dispersal failure.

Although New Zealand has lost 80% of its flightless birds, including all nine moa, some extant species may still perform important seed dispersal services. Kiwi (*Apteryx spp.*), weka, and kākāpō (*Strigops habroptilus*) have all been recorded consuming fruits and dispersing the seeds intact (Clout and Hay 1989), although kākāpō destroy most seeds larger than 3 mm. Weka in particular have a diet which is seasonally high in fruit and have been recorded consuming the fruits of over 26 plant species, so they could make significant contributions to seed dispersal (Beauchamp, 1987; Beauchamp et al., 1999; Clout et al., 1989; Coleman et al., 1983). However, the potential seed dispersal capabilities of weka have been overlooked so far, and no research has been conducted into their effectiveness as seed dispersers. Information on the seed dispersal capabilities of weka may also give valuable insights into the roles played by extinct flightless rails, of which New Zealand has lost five species (Flemings rail *Pleistorallus flemingi*, Snipe-rail *Capellirallus karamu*, Hawkins' rail *Diaphorapteryx hawkinsi*, Dieffenbach's rail *Gallirallus dieffenbachii*, Chatham Island rail *Cabalus modestus* – the latter three are Chatham Island endemics) and the Pacific as a whole has lost >450 (Steadman 2006).

Table 1.1. *Mean mass of New Zealand (North and South Islands) avian frugivore community before and after human arrival. All birds that include fruit in their diet are included. Mean mass for each species is the mean of the male and female weights (weights and dietary information from nzbirdsonline.org.nz).* † *denotes extinct species.*

Species	Mean mass (kg)	Prehuman	Posthuman
Banded rail *Gallirallus philippensis*	0.17	Y	Y
Bellbird *Anthornis melanura*	0.03	Y	Y
Brown creeper *Mohoua novaeseelandiae*	0.023	Y	Y
Great spotted kiwi *Apteryx haastii*	2.6	Y	Y
Hihi *Notiomystis cincta*	0.033	Y	Y
Kākāpō *Strigops habroptilus*	2.5	Y	Y
Kea *Nestor notabilis*	0.9	Y	Y
Kererū *Hemiphaga novaeseelandiae*	0.63	Y	Y
Little spotted kiwi *Apteryx owenii*	1.25	Y	Y
Mohua *Mohoua ochrocephala*	0.028	Y	Y
North Island brown kiwi *Apteryx mantelli*	2.35	Y	Y
North Island kōkako *Callaeas wilsoni*	0.225	Y	Y
North Island robin *Petroica longipes*	0.035	Y	Y
North Island tīeke *Philesturnus rufusater*	0.07	Y	Y
Rock wren *Xenicus gilviventris*	0.018	Y	Y
Rowi *Apteryx rowi*	2.25	Y	Y
South Island robin *Petroica australis*	0.035	Y	Y
South Island tīeke *Philesturnus carunculatus*	0.075	Y	Y
Tokoeka *Apteryx australis*	2.75	Y	Y
Tūī *Prosthemadera novaeseelandiae*	0.11	Y	Y
Weka *Gallirallus australis*	1	Y	Y
Whitehead *Mohoua albicilla*	0.0165	Y	Y
Crested moa† *Pachyornis australis*	67	Y	N
Eastern moa† *Emeus crassus*	57.5	Y	N
Heavy-footed moa† *Pachyornis elephantopus*	118	Y	N
Huia† *Heteralocha acutirostris*	0.35	Y	N
Little bush moa† *Anomalopteryx didiformis*	26.5	Y	N
Mantell's moa† *Pachyornis geranoides*	26.5	Y	N
North Island giant moa† *Dinornis novaezealandiae*	138	Y	N
North Island piopio† *Turnagra tanagra*	0.13	Y	N
New Zealand raven† *Corvus antipodum*	0.975	Y	N
South Island giant moa† *Dinornis robustus*	142	Y	N
South Island kōkako† *Callaeas cinerea*	0.225	Y	N
South Island piopio† *Turnagra capensis*	0.13	Y	N
Stout-legged moa† *Euryapteryx curtus*	60.5	Y	N
Upland moa† *Megalapteryx didinus*	54	Y	N
Mean mass of frugivore community (kg)		**19.69**	**0.78**

Human arrival in New Zealand therefore precipitated a suite of extinctions across the avian frugivore community, which (as elsewhere across the globe) resulted in a disproportionate loss of the largest frugivores. If we use the calculation methods of Heinen et al. (2018), then these extinctions meant that the mean mass of the avian frugivore community decreased from 19.69 kg in prehuman times, to a mere 0.78 kg following human arrival – a downsizing of 96% (Table 1.1). As large frugivores typically have more obligate relationships with large seeds (e.g. Meehan et al. 2002), this downsizing of the avian frugivore community could have resulted in impaired dispersal of New Zealand's largest seeds. This possible loss of interactions between large frugivores and large seeds could be further exacerbated by declines in kererū abundance. Kererū are a putative keystone frugivore (Clout and Hay 1989) that are currently the primary or only disperser for six large-seeded plants: tawa *(Beilschmiedia tawa*), taraire (*Beilschmiedia taraire*), puriri (*Vitex lucens*), karaka (*Corynocarpus laevigatus*), *Elingamita johnsonii*, and tawapou (*Pouteria costata*) (Kelly et al. 2010; Bellingham et al. 2010). The widespread distribution, mobility, large gape, and catholic diet (which includes the fruits of over 70 plant species) of kererū make them a significant seed disperser (McEwen 1978; Clout and Hay 1989). Kererū have suffered major declines since human arrival and continue to suffer from mammalian predation (Clout et al. 1995; Mander et al. 1998; Innes et al. 2010), but their more recent population trends are surprisingly unstudied, although Robertson et al. (2007) list them as increasing in distribution since the 1980s. These recent population trends are expected to have important ramifications for kererū's seed dispersal capacities, and the dispersal of large seeds in New Zealand.

Lastly, the introduction of mammalian predators to New Zealand affected plant recruitment directly, through seed and seedling predation. Rats can depress plant recruitment by eating fallen fruit and eating fruit from the tree crown, thereby reducing the fruit crop available to dispersers, and eating seedlings. Beveridge (1964) found that rats destroyed a large proportion of the rimu (*Dacrydium cupressinum*) crop in a mast year, sparking concern for how rodents might be affecting the regeneration of New Zealand forests. While Moles and Drake (1999) found low levels of post-dispersal rodent seed predation for 11 plant species in a short term study in a heavily

modified urban forest remnant, Campbell and Atkinson (2002) recorded Polynesian rats depressing recruitment of several tree species on New Zealand's northern offshore islands. On Breaksea Island seedling numbers of various species increased substantially following the eradication of Norway rats in 1988 (Allen et al. 1994). However, native seed predators such as kākāriki (*Cyanoramphus spp.*) and kākā (*Nestor meridionalis*) may have also driven high levels of seed predation in prehuman times (e.g. Beveridge 1964), and it is possible that rodent seed predation is numerically analogous to those levels.

Despite these avian declines, extinctions, and possibly elevated modern-day seed predation rates, it is still unclear whether seed dispersal in New Zealand is at risk. Although a review by Clout and Hay (1989) argued that New Zealand seed dispersal services may be at risk, ten studies on fruit removal rates for various New Zealand plant species (Kelly et al. 2010) showed that seven species seemed to show reasonably good dispersal, two species had slowed dispersal (*Fuchsia excorticata* and *Rhopalostylis sapida*), and only one species was dispersal limited (*Pittosporum crassifolium*). Since then, Wotton and Kelly (2011) demonstrated that the synergistic effects of frugivore loss and mammalian seed predation might be severely reducing recruitment in taraire (*Beilschmiedia tarairi*) and karaka (*Corynocarpus laevigatus*). Similarly, large-seeded species on the Three Kings Islands were unable to regenerate away from parent trees until kererū recolonised the area (Bellingham et al. 2010). Young et al. (2012) also found that the majority of seed dispersal services in alpine ecosystems were reliant on the nationally endangered kea. However, the state of seed dispersal in New Zealand is still largely unknown.

New Zealand seed dispersal networks may be resilient to frugivore loss if they feature high levels of redundancy, e.g. several birds performing the same seed dispersal services. However, while there may be diffuse relationships between New Zealand's frugivorous birds and the plant species they disperse (e.g. wide dietary overlap), each bird may still provide very different dispersal quality. Accurate measures of seed dispersal effectiveness must take both metrics into account, but very few studies have measured the dispersal quality provided by New Zealand birds. Understanding whether some frugivores provide unique dispersal services would give a more

comprehensive understanding of redundancy in New Zealand seed dispersal networks, and therefore deeper insights into how vulnerable the networks are to species loss.

1.4 Thesis outline

The overall objective of this thesis is to assess the impact of avian declines and extinctions on seed dispersal in New Zealand. I have tackled this objective by broadly focusing on several 'pinchpoints' in New Zealand's contemporary seed dispersal network (Fig. 1.1). These pinchpoints are the loss of New Zealand's largest frugivores and their potential interactions with large seeds, the current health of kererū populations, and the gap in knowledge regarding the importance of extant flightless birds for seed dispersal. Because each chapter has been written in a suitable format for submission to a journal, Figures and Tables are numbered within each chapter, and appendices and references are included at the end of that chapter. There also may be a small amount of inevitable repetition between chapters, particularly in the various introductions.

In Chapter 2, I begin by assessing trends in kererū abundance and dispersal of six plant species at Pelorus, over three decades. While this is a site-specific study, the findings have implications for kererū abundances and their impact on seed dispersal across New Zealand.

In Chapter 3, I analyse moa coprolites (subfossilised droppings) and subfossilised gizzards to investigate whether moa were important dispersers of large seeds in prehuman New Zealand. This research tests whether the loss of moa has created a gap in the dispersal of large seeds.

In Chapter 4, I assess the importance of weka for seed dispersal of hīnau by comparing hīnau dispersal from the ground and the canopy across mainland and offshore island bird sanctuary sites. This also allowed me to investigate the impact of both native and exotic seed predators on hīnau dispersal, and to see whether hīnau was suffering from dispersal failure on the mainland of New Zealand.

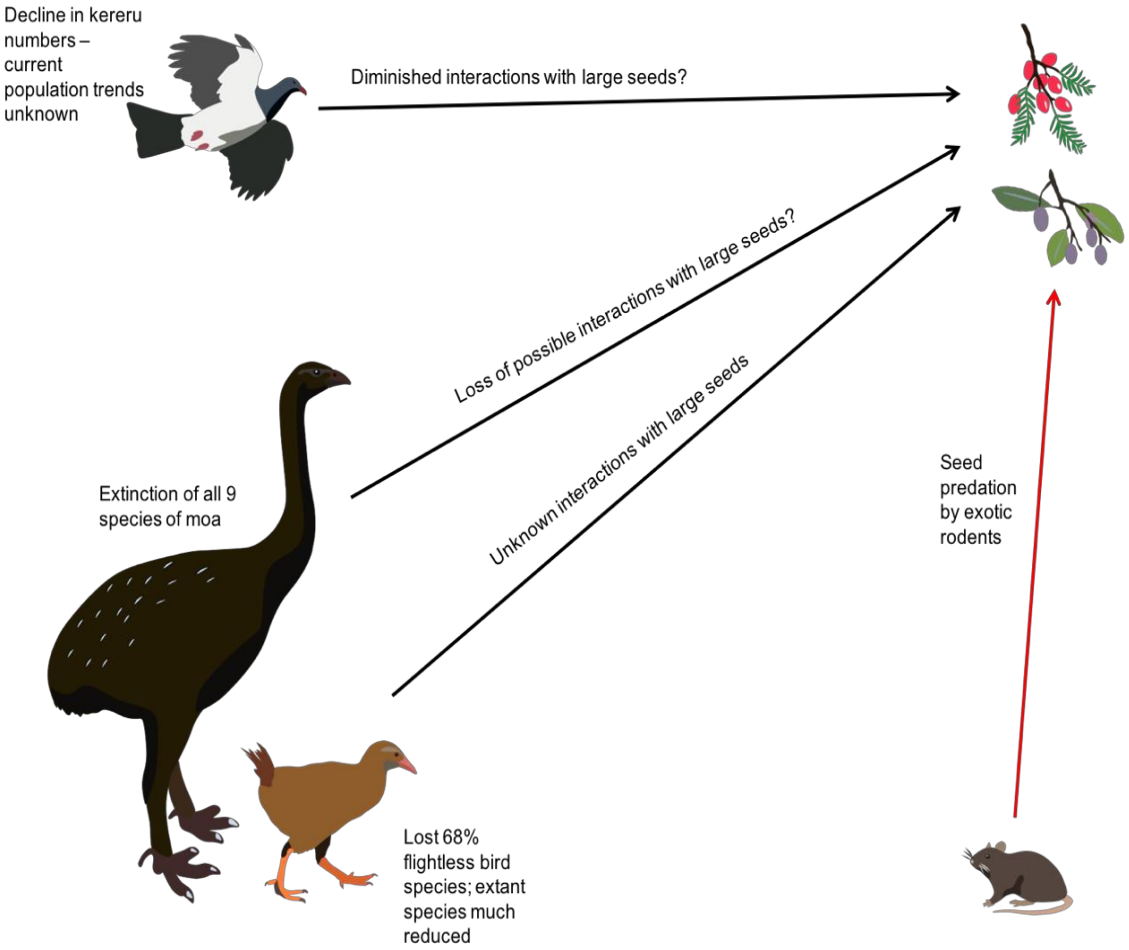


Figure 1.1. *Conceptual figure showing possible pinchpoints for New Zealand's contemporary seed dispersal networks.*

In Chapter 5, I estimate seed retention times for weka for two large seeded species, an important component of seed dispersal quality. Understanding the quality of seed dispersal provided by weka helps to determine whether weka offer unique dispersal services compared to other extant frugivores.

In Chapter 6, I use a mechanistic model approach to assess the distance that weka disperse miro and hīnau seeds, another important element of seed dispersal quality. Specifically, I assess whether weka that frequently interact with people disperse seeds shorter distances than their more remote counterparts. New Zealand is becoming an increasingly crowded place, and this may affect frugivorous birds' behaviour and alter the seed dispersal services they provide.

Finally, in Chapter 7 I synthesize my findings to assess how avian declines and extinctions have affected seed dispersal in New Zealand. In particular, I focus on whether we should be concerned about the dispersal of large seeds, and the relative contributions of New Zealand's frugivorous birds to seed dispersal services.

1.5 References

Allen RB, Lee WG, Rance BD (1994) Regeneration in indigenous forest after eradication of Norway rats, Breaksea Island, New Zealand. New Zeal J Bot 32:429–439 . doi: 10.1080/0028825X.1994.10412930

Beauchamp A (1987) A population study of the weka, Gallirallus australis, on Kapiti Island. Victoria University of Wellington

Beauchamp AJ, Butler DJ, King D (1999) Weka (Gallirallus australis) recovery plan 1999-2009. Threatened Species Recovery Plan 29.

Bellingham PJ, Wiser SK, Wright AE, et al (2010) Disperser communities and legacies of goat grazing determine forest succession on the remote Three Kings Islands, New Zealand. Biol Conserv 143:926–938 . doi: 10.1016/j.biocon.2010.01.001

Beveridge AE (1964) Dispersal and destruction of seed in central North Island podocarp forest. Proc New Zeal Ecol Soc 11:48–55

Blake S, Wikelski M, Cabrera F, et al (2012) Seed dispersal by Galápagos tortoises. J Biogeogr 39:1961–1972 . doi: 10.1111/j.1365-2699.2011.02672.x

Boyer AG (2010) Consistent ecological selectivity through time in Pacific Island avian extinctions. Conserv Biol 24:511–519 . doi: 10.1111/j.1523-1739.2009.01341.x

Brodie JF, Helmy OE, Brockelman WY, Maron JL (2009) Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. Ecol Appl 19:854–863 . doi: 10.1890/08-0955.1

Burrows C. (1994) Fruit, seeds, birds and the forests of Banks Peninsula. New Zeal Nat Sci 21:87–108

Campbell DJ, Atkinson IAE (2002) Depression of tree recruitment by the Pacific rat (Rattus exulans Peale) on New Zealand's northern offshore islands. Biol Conserv 107:19–35 . doi: 10.1016/S0006-3207(02)00039-3

Caves EM, Jennings SB, HilleRisLambers J, et al (2013) Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. PLoS One 8: . doi: 10.1371/journal.pone.0065618

Chimera CG, Drake DR (2010) Patterns of seed dispersal and dispersal failure in a Hawaiian dry forest having only introduced birds. Biotropica 42:493–502 . doi: 10.1111/j.1744-7429.2009.00610.x

Christian CE (2001) Consequences of a biological invasion reveal the importance of

mutualism for plant communities. Nature 413:635–639 . doi: 10.1038/35098093

Clout MN, Hay JR (1989) The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. N Z J Ecol 27–33 . doi: 10.2307/24053245

Clout MN, Karl BJ, Pierce RJ, Robertson HA (1995) Breeding and survival of New Zealand Pigeons Hemiphaga novaeseelandiae. Ibis (Lond 1859) 137:264–271 . doi: 10.1111/j.1474-919X.1995.tb03248.x

Coleman JD, Warburton B, Green WQ (1983) Some population statistics and movements of the Western Weka. Notornis 30:93–107

Comita LS, Queenborough SA, Murphy SJ, et al (2014) Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. J Ecol 102:845–856 . doi: 10.1111/1365-2745.12232

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp 298–312

Cordeiro NJ, Howe HF (2001) Low recruitment of trees dispersed by animals in African forest fragments. Conserv Biol 15:1733–1741 . doi: 10.1046/j.1523-1739.2001.99579.x

Corlett RT (2007) Pollination or seed dispersal: Which should we worry about most? In: Seed Dispersal: Theory and Its Application in a Changing World. pp 523–544

Correa SB, Arujo JK, Penha J, et al (2016) Stability and generalization in seed dispersal networks: A case study of frugivorous fish in Neotropical wetlands. Proc R Soc B Biol Sci 283:20161267 . doi: 10.1098/rspb.2016.1267

Cosyns E, Delporte A, Lens L, Hoffmann M (2005) Germination success of temperate grassland species after passage through ungulate and rabbit guts. J Ecol 93:353–361 . doi: 10.1111/j.0022-0477.2005.00982.x

Daniel MJ (1976) Feeding by the short-tailed bat (Mystacina tuberculata) on fruit and possibly nectar. New Zeal J Zool 3:391–398 . doi: 10.1080/03014223.1976.9517927

De Vega C, Arista M, Ortiz PL, et al (2011) Endozoochory by beetles: A novel seed dispersal mechanism. Ann Bot 107:629–637 . doi: 10.1093/aob/mcr013

Duthie C, Gibbs G, Burns KC (2006) Seed dispersal by weta. Science (80-) 311:1575 . doi: 10.1126/science.1123544

Egerer MH, Fricke EC, Rogers HS (2018) Seed dispersal as an ecosystem service: frugivore loss leads to decline of a socially valued plant, Capsicum frutescens. Ecol Appl 28:655–667 . doi: 10.1002/eap.1667

Forsyth DM, Allen RB, Wilmshurst JM, Coomes D (2010) Have deer replaced moa? A review of the impacts of introduced deer on New Zealand ecosystems. N Z J Ecol 34:48

Fricke EC, Bender J, Rehm EM, Rogers HS (2018) Functional outcomes of mutualistic network interactions: a community-scale study of frugivore gut passage on germination. J Ecol 1–11 . doi: 10.1111/1365-2745.13108

Galetti M, Donatti CI, Pizo MA, Giacomini HC (2008) Big fish are the best: Seed dispersal of Bactris glaucescens by the pacu fish (Piaractus mesopotamicus) in the Pantanal, Brazil. Biotropica 40:386–389 . doi: 10.1111/j.1744-7429.2007.00378.x

Garcia D, Martinez D (2012) Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. Proc R Soc B Biol Sci 22:13–18 . doi: 10.1098/rspb.2012.0175

Godinez-Alvarez AH, Valiente-banuet A, Rojas-martinez A, et al (2009) The role of seed dispersers in the population dynamics of the columnar cactus Neobuxbaumia tetetzo. Ecology 83:2617–2629

Green AK, Ward D, Griffiths ME (2009) Directed dispersal of mistletoe (Plicosepalus acaciae) by Yellow-vented Bulbuls (Pycnonotus xanthopygos). J Ornithol 150:167–173 . doi: 10.1007/s10336-008-0331-9

Heinen JH, van Loon EE, Hansen DM, Kissling WD (2018) Extinction-driven changes in frugivore communities on oceanic islands. Ecography (Cop) 41:1245–1255 . doi: 10.1111/ecog.03462

Herrera CM, Pellmyr O (eds) (2009) Plant Animal Interactions: An Evolutionary Approach. John Wiley & Sons

Hirsch BT, Kays R, Pereira VE, Jansen PA (2012) Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. Ecol Lett 15:1423–1429 . doi: 10.1111/ele.12000

Howe HF (1986) Seed Dispersal by Fruit-Eating Birds and Mammals. In: Seed Dispersal. pp 123–189

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol Syst 13:201–228 . doi: 10.1146/annurev.es.13.110182.001221

Innes J, Kelly D, Overton JMC, Gillies C (2010) Predation and other factors currently limiting

New Zealand forest birds. N. Z. J. Ecol. 34:86–114

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528 . doi: 10.1086/282687

Janzen DH, Miller GA, Hackforth-Jones J, et al (1976) Two Costa Rican bat-generated seed shadows of Andira Inermis (Leguminosae). Ecology 57:1068–1075 . doi: 10.2307/1941072

Jerozolimski A, Ribeiro MBN, Martins M (2009) Are tortoises important seed dispersers in Amazonian forests? Oecologia 161:517–528 . doi: 10.1007/s00442-009-1396-8

Jordano P, Garcia C, Godoy JA, Garcia-Castano JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. Proc Natl Acad Sci 104:3278–3282 . doi: 10.1073/pnas.0606793104

Kelly D, Ladley JJ, Robertson AW, et al (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit- dispersal in New Zealand. N Z J Ecol 34:66–85

Kelly D, Robertson AW, Ladley JJ, et al (2006) Relative (un)importance of introduced animals as pollinators and dispersers of native plants. In: Biological Invasions in New Zealand. pp 227–245

Kwit C, Levey DJ, Turner SA, et al (2007) Out of one shadow and into another: causes and consequences of spatially contagious seed dispersal by frugivores. In: Dennis A, Schupp E, Green R, Westcott D (eds) Seed Dispersal: Theory and its Application in a Changing World. CAB International, Wallingford, UK, pp 427–444

Lee WG, Clout MN, Robertson HA, Bastow Wilson J (1991) Avian dispersers and fleshy fruits in New Zealand. Proc Int Orn Congr XX 1617–1623

Levine JM, Murrell DJ (2003) The Community-Level Consequences of Seed Dispersal Patterns. Annu Rev Ecol Evol Syst 34:549–574 . doi: 10.1146/annurev.ecolsys.34.011802.132400

Lord J (2002) Have frugivores influenced the evolution of fruit traits in New Zealand? In: DJ L, WR S, M G (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, WallingfoRd, UK, pp 55–68

Lord JM (1991) Pollination and seed dispersal in Freycinetia baueriana, a dioecious liane that has lost its bat pollinator. New Zeal J Bot 29:83–86 . doi: 10.1080/0028825X.1991.10415545

Mander C, Hay R, Powlesland R (1998) Monitoring and management of kereru (Hemiphaga

novaeseelandiae)

McConkey KR, Prasad S, Corlett RT, et al (2012) Seed dispersal in changing landscapes. Biol. Conserv. 146:1–13

McEwen WM (1978) The food of the New Zealand pigeon (Hemiphaga novaeseelandiae novaeseelandiae). N Z J Ecol 1:99–108 . doi: 10.1002/jid

Meehan HJ, McConkey KR, Drake DR (2002) Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. J Biogeogr 29:695–712 . doi: 10.1046/j.1365-2699.2002.00718.x

Mello MAR, Marquitti FMD, Guimarães PR, et al (2011) The missing part of seed dispersal networks: Structure and robustness of bat-fruit interactions. PLoS One 6:e17395 . doi: 10.1371/journal.pone.0017395

Moles AT, Drake DR (1999) Post-dispersal seed predation on eleven large-seeded species from the New Zealand flora: A preliminary study in secondary forest. New Zeal J Bot 37:679–685 . doi: 10.1080/0028825X.1999.9512662doi.org/10.1080/0028825X.1999.9512662

O'Farrill G, Galetti M, Campos-Arceiz A (2013) Frugivory and seed dispersal by tapirs: An insight on their ecological role. Integr. Zool. 8:4–17

Olesen JM, Valido A (2003) Lizards as pollinators and seed dispersers: An island phenomenon. Trends Ecol. Evol. 18:177–181

Pejchar L (2015) Introduced birds incompletely replace seed dispersal by a native frugivore. AoB Plants 7: . doi: 10.1093/aobpla/plv072

Pérez-Méndez N, Jordano P, García C, Valido A (2016) The signatures of Anthropocene defaunation: Cascading effects of the seed dispersal collapse. Sci Rep 6:24820 . doi: 10.1038/srep24820

Pérez-Méndez N, Jordano P, Valido A (2015) Downsized mutualisms: Consequences of seed dispersers' body-size reduction for early plant recruitment. Perspect Plant Ecol Evol Syst 17:151–159 . doi: 10.1016/j.ppees.2014.12.001

Perry GLW, Wheeler AB, Wood JR, Wilmshurst JM (2014) A high-precision chronology for the rapid extinction of New Zealand moa (Aves, Dinornithiformes). Quat Sci Rev 105:126–135 . doi: 10.1016/j.quascirev.2014.09.025

Robertson AW, Trass A, Ladley JJ, Kelly D (2006) Assessing the benefits of frugivory for seed germination: The importance of the deinhibition effect. Funct. Ecol. 20:58–66

Robertson C, Hyvőnen P, Fraser MJ, Pickard CR (2007) Atlas of Bird Distribution in New

Zealand 1999-2004. Ornithological Society of New Zealand

Rodríguez-Cabal MA, Aizen MA, Novaro AJ (2007) Habitat fragmentation disrupts a plant-disperser mutualism in the temperate forest of South America. Biol Conserv 139:195–202 . doi: 10.1016/j.biocon.2007.06.014

Rodríguez-Pérez J, Traveset A (2010) Seed dispersal effectiveness in a plant-lizard interaction and its consequences for plant regeneration after disperser loss. Plant Ecol 207:269–280 . doi: 10.1007/s11258-009-9671-7

Rogers HS, Buhle ER, HilleRisLambers J, et al (2017) Effects of an invasive predator cascade to plants via mutualism disruption. Nat Commun 8:14557 . doi: 10.1038/ncomms14557

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: A conceptual review. New Phytol. 188:333–353

Sekercioglu CH, Daily GC, Ehrlich PR (2004) Ecosystem consequences of bird declines. Proc Natl Acad Sci 101:18042–18047 . doi: 10.1073/pnas.0408049101

Steadman DW (2006) Extinction and biogeography of tropical Pacific birds. University of Chicago Press, Chicago

Stiles EW (2000) Animals as seed dispersers. Seeds Ecol Regen Plant Communities 111–124 . doi: 10.1111/ecoj.12105

Terborgh J, Nuñez-Iturri G, Pitman NCA, et al (2008) Tree recruitment in an empty forest. Ecology 89:1757–1768 . doi: 10.1890/07-0479.1

Thorsen MJ, Seddon PJ, Dickinson KJM (2011) Faunal influences on New Zealand seed dispersal characteristics. Evol Ecol 25:1397–1426 . doi: 10.1007/s10682-011-9470-1

Timóteo S, Ramos JA, Vaughan IP, Memmott J (2016) High resilience of seed dispersal webs highlighted by the experimental removal of the dominant disperser. Curr Biol 26:910–915 . doi: 10.1016/j.cub.2016.01.046

Tjelele J, Ward D, Dziba L (2015) The effects of seed ingestion by livestock, dung fertilization, trampling, grass competition and fire on seedling establishment of two woody plant species. PLoS One 10:e0117788 . doi: 10.1371/journal.pone.0117788

Towns DR, Broome KG (2003) From small Maria to massive Campbell: Forty years of rat eradications from New Zealand islands. New Zeal J Zool 30:377–398 . doi: 10.1080/03014223.2003.9518348

Trakhtenbrot A, Nathan R, Perry G, Richardson DM (2005) The importance of long-distance dispersal in biodiversity conservation. Divers Distrib 11:173–181 . doi:

10.1111/j.1366-9516.2005.00156.x

Traveset A (1998) Effect of seed passage through vertebrate frugivores' guts on germination: A review. Perspect Plant Ecol Evol Syst 1:151–190 . doi: 10.1078/1433-8319-00057

Traveset A, Robertson AW, Rodríguez-Pérez J (2007) A review on the role of endozoochory in seed germination. In: Dennis AJ, Schupp EW, Green RJ, Westcott DA (eds) Seed Dispersal: Theory and Its Application in a Changing World. CABI International, Wallingford, UK, pp 78–103

Traveset A, Verdú M (2002) A meta-analysis of the effect of gut treatment on seed germination. In: Levey DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CABI International, Wallingford, UK, pp 339–350

Vander Wall SB (2001) The evolutionary ecology of nut dispersal. Bot. Rev. 67:74–117

Vanthomme H, Bellé B, Forget PM (2010) Bushmeat hunting alters recruitment of large-seeded plant species in Central Africa. Biotropica 42:672–679 . doi: 10.1111/j.1744-7429.2010.00630.x

Wandrag EM, Dunham AE, Duncan RP, Rogers HS (2017) Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings. Proc Natl Acad Sci 114:201709584 . doi: 10.1073/pnas.1709584114

Wenny DG (2001) Advantages of seed dispersal: A re-evaluation of directed dispersal. Evol Ecol Res 3:51–74 . doi: 10.1002/(SICI)1098-2345(200004)50:4<275::AID-AJP4>3.0.CO;2-K

Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH (2008) Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. Proc Natl Acad Sci 105:7676–7680 . doi: 10.1073/pnas.0801507105

Wilmshurst JM, Higham TFG (2004) Using rat-gnawed seeds to independently date the arrival of Pacific rats and humans in New Zealand. The Holocene 14:801–806

Wood JR, Rawlence NJ, Rogers GM, et al (2008) Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes). Quat Sci Rev 27:2593–2602 . doi: 10.1016/j.quascirev.2008.09.019

Wotton DM, Drake DR, Powlesland RG, Ladley JJ (2016) The role of lizards as seed dispersers in New Zealand. J. R. Soc. New Zeal. 46:40–65

Wotton DM, Kelly D (2011) Frugivore loss limits recruitment of large-seeded trees. Proc R Soc B Biol Sci 278:3345–3354 . doi: 10.1098/rspb.2011.0185

Wyman TE, Trewick SA, Morgan-Richards M, Noble ADL (2011) Mutualism or opportunism? Tree fuchsia (Fuchsia excorticata) and tree weta (Hemideina) interactions. Austral Ecol 36:261–268 . doi: 10.1111/j.1442-9993.2010.02146.x

Yoshikawa T, Isagi Y (2012) Dietary breadth of frugivorous birds in relation to their feeding strategies in the lowland forests of central Honshu, Japan. Oikos 121:1041–1052 . doi: 10.1111/j.1600-0706.2011.19888.x

Young LM, Kelly D, Nelson XJ (2012) Alpine flora may depend on declining frugivorous parrot for seed dispersal. Biol Conserv 147:133–142 . doi: 10.1016/j.biocon.2011.12.023

UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

Deputy Vice-Chancellor's Office
Postgraduate Research Office

Co-Authorship Form

This form is to accompany the submission of any thesis that contains research reported in co-authored work that has been published, accepted for publication, or submitted for publication. A copy of this form should be included for each co-authored work that is included in the thesis. Completed forms should be included at the front (after the thesis abstract) of each copy of the thesis submitted for examination and library deposit.

Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter 2: Published in the New Zealand Journal of Ecology

Carpenter JK, Kelly D, Clout MN, Karl BJ, Ladley LL. 2017. "Trends in the detection of a large-frugivore(Hemiphaga novaeseelandiae) and fleshy-fruited seed dispersal over three decades." New Zealand Journal of Ecology 41(1): 41-46

Please detail the nature and extent (%) of contribution by the candidate:

Jo Carpenter developed the study questions, analysed the data, created graphs (with the exception of Fig 2, which was created by Dave Kelly), and wrote the manuscript (50%)

Certification by Co-authors:

If there is more than one co-author then a single co-author can sign on behalf of all

The undersigned certifies that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name: Dave Kelly	Signature: Dave Kelly	Date: *6/2/2019*

2

Trends in the detections of a large frugivore (*Hemiphaga novaeseelandiae*) and fleshy-fruited seed dispersal over three decades

Podocarp-broadleaf forest at Pelorus Bridge. Credit: Dave Kelly

2.1 Abstract

The kererū (*Hemiphaga novaeseelandiae*) is a large fruit pigeon that in New Zealand is an important seed disperser for native plant species. However, little is known about recent changes in kererū densities and how these changes might affect seed dispersal services. I used long-term kererū counts and seedfall trap data from Pelorus in Marlborough to measure trends in bird abundance and seed dispersal. Using monthly kererū counts from 1983–1989 and 2002–2006, I found that counts significantly decreased between the two decades. Most of this decline was driven by changes in the seasonal abundance of kererū : a pronounced late-winter/spring peak in numbers in the 1980s had almost vanished by the 2000s. The late-winter/spring increase in kererū in the 1980s was probably driven by kererū moving into the area to feed on lowland foliage. Therefore, the reduction of late-winter/spring kererū in the 2000s could be driven by either a change in regional movement patterns or an authentic decline in the kererū population. Seedfall data for six fleshy-fruited trees (tawa *Beilschmiedia tawa*, miro *Prumnopitys ferruginea*, matai *Prumnopitys taxifolia*, hinau *Elaeocarpus dentatus*, rimu *Dacrydium cupressinum*, and kahikatea *Dacrycarpus dacrydioides*) from 1986–1990 and 2004–2010 allowed estimation of the percentage of each fruit crop handled by frugivores (an index of dispersal quantity). I found that the percentage of seeds handled by frugivores was higher in the 2000s than in the 1980s for tawa, and lower for matai. Seed handling rates were unchanged between the two decades for miro, hinau, rimu, and kahikatea. Over this time period there was no overall worsening in dispersal quantity between the two decades, probably because kererū numbers did not change significantly during the autumn fruiting season, and because other birds could be important dispersers for smaller-seeded species.

2.2 Introduction

Habitat loss, illegal harvesting, and invasive species have resulted in global declines of frugivores, generating concern for seed dispersal services (Sekercioglu et al. 2004). Large-bodied avian frugivores are particularly susceptible to decline, due to their typically lower population densities, larger home ranges, and lower reproductive rates (Boyer 2010). Many trees have frugivore-dispersed seeds, so frugivores play an important role in the maintenance of plant communities. For example, over 59% of trees and 48% of all woody plants in New Zealand produce frugivore-dispersed fruits (Burrows 1994; Kelly et al. 2010).

The New Zealand pigeon, or kererū (*Hemiphaga novaeseelandiae*), is a large-bodied (c. 650 g; Clout et al. 1992) endemic New Zealand frugivore. Kererū historically suffered major declines due to hunting, but have been protected by law since 1921, resulting in them persisting in most districts that contain remnants of lowland forest (Clout et al. 1995). The contemporary threats they face are predation by introduced predators, poaching, and occasional episodes of mortality in late winter and early spring, possibly due to degraded habitat and subsequent poor nutrition (Clout et al. 1995). The International Union for Conservation of Nature and Miskelly et al. (2008) list them as near threatened and not threatened respectively, yet surprisingly little is known about their more recent population trends. Several kererū populations studied in the 1990s appeared to be highly susceptible to ongoing decline due to their high mortality rates and low reproductive success (Pierce and Graham 1995; Clout et al. 1995). Despite these worrying observations, the distribution of kererū appears to be increasing, with kererū occupying 58.1% of national grid squares from 1999 to 2004 (Robertson et al. 2007), up from 46.6% between 1969 and 1979 (Bull et al. 1985), although survey effort differed between the two time periods.

Kererū are frequently cited as a keystone species pivotal to the health of podocarp-broadleaf forests due to their widespread distribution, mobility, and diverse diet, which includes fruits from over 70 plant species (McEwen 1978; Clout and Hay 1989), although smaller native birds also make important contributions to dispersal (Kelly et al. 2010). Kererū are the primary disperser for New Zealand's six largest-seeded native

plants: tawa (*Beilschmiedia tawa*), taraire (*Beilschmiedia tarairi*), puriri (*Vitex lucens*), karaka (*Corynocarpus laevigatus*), *Elingamita johnsonii* and tawapou (*Planchonella costata*). Therefore, fluctuations in kererū numbers are expected to have important ramifications for seed dispersal services. The percentage of a fruit crop that has passed through an animal (fruit-handling) is related to dispersal quantity, which is an important indicator of the status of dispersal interactions (Wyman 2013). Surprisingly, there are only a handful of studies of dispersal quantity in New Zealand, the majority of which found adequate dispersal rates (Kelly et al. 2010). However, it appears that the mainland (North, South, and Stewart Islands) has slower or poorer fruit removal rates compared to island sanctuaries that retain higher bird densities (McNutt 1998; Robertson et al. 2008; Iles 2012). As reductions in dispersal services may have negative consequences for plant regeneration (Wotton and Kelly 2011), evaluating long-term trends in both dispersal quantity and kererū abundances on the mainland is important.

I used two long-term datasets to measure changes in bird abundance and fruit handling in the Pelorus Bridge area, Marlborough. One was a dataset of monthly kererū counts from 1983–1989 and 2002–2006. The other was indices of annual seedfall data for six fleshy-fruited trees (rimu (*Dacrydium cupressinum*), kahikatea (*Dacrycarpus dacrydioides*), miro (*Prumnopitys ferruginea*), matai (*Prumnopitys taxifolia*) (all Podocarpaceae), tawa (*Beilschmiedia tawa*, Lauraceae), and hīnau (*Elaeocarpus dentatus*, Elaeocarpaceae)) from 1986–1990 and 2004–2010. My research aimed to answer the following questions: (1) have kererū detections changed in the Pelorus area between the 1980s and 2000s, both overall and seasonally, and (2) is there a change in the percentage of fruits handled by frugivores (an index of dispersal quantity) for the six plant species between the 1980s and 2000s.

2.3 Methods

2.3.1 Study site

All seed trap data and some kererū data were collected from Pelorus Bridge Scenic Reserve (41°18' S, 173°35' E) in Marlborough. The 1750 ha reserve is a lowland (~50 m a.s.l.) remnant of old-growth, tawa-podocarp forest, contiguous with Mt Richmond

Forest Park to the southwest. It contains stands of matai and kahikatea, with miro, totara (*Podocarpus totara*), rimu, and hīnau, mixed with dense areas of tawa, kāmahi (*Weinmannia racemosa*), and beech (*Fuscospora* spp.). No five-minute bird counts were conducted at the site, but other important avian frugivores such as tūī (*Prosthemadera novaeseelandiae*), bellbirds (*Anthornis melanura*), and silvereyes (*Zosterops lateralis*) are present in the general area (Robertson et al. 2007). Additional kererū data were collected from sites in Rai Valley (41°13’ S, 173°34’ E), Marlborough, immediately north of Pelorus Bridge. Rai Valley is a lowland river valley (~40 m a.s.l.) that predominantly consists of pastureland on the river flats, scrubby hillsides, and mature podocarp-broadleaf forest at higher altitudes. Some podocarp-broadleaf forest fragments remain within the cleared land, and there are also several *Pinus* plantations.

2.3.2 Kererū counts

I used a 12-year dataset of monthly kererū counts conducted by one observer (Brian Karl) at Rai Valley from July 1983 to December 1989 and from January 2002 to June 2006. Counts comprised walking and driving transects. These were done in the morning (0930–1200 hrs) and repeated in the reverse direction in the afternoon (1300–1530 hrs). Each time a transect was walked or driven it was considered a count. A bird that was seen or heard (typically flying) was counted. Any bird that was considered to have already been counted was not included again in the count tally. Thus the transect counts were of individual birds and not the number of encounters of kererū.

Walking counts were made while walking slowly along forest tracks or along a road (Fig. 2.1). Habitats sampled in these areas include: (A) Pelorus Bridge Scenic Reserve, a bush track walk through mature beech-podocarp-broadleaf forest, dominated by rimu, kahikatea, matai, miro, tawa, kāmahi and *Coprosma* spp.; (B) Carluke Reserve, a small (~15 ha) remnant kahikatea and matai-dominant forest patch with a riparian strip of exotic deciduous willow (*Salix* spp.), poplar (*Populus* spp.) and native kōwhai (*Sophora* spp.) trees alongside the Rai river; and (C) Bulford, a ~1.0 km road walk surveying open pasture land and a riparian strip comprising mostly willow, kōwhai, and beech trees.

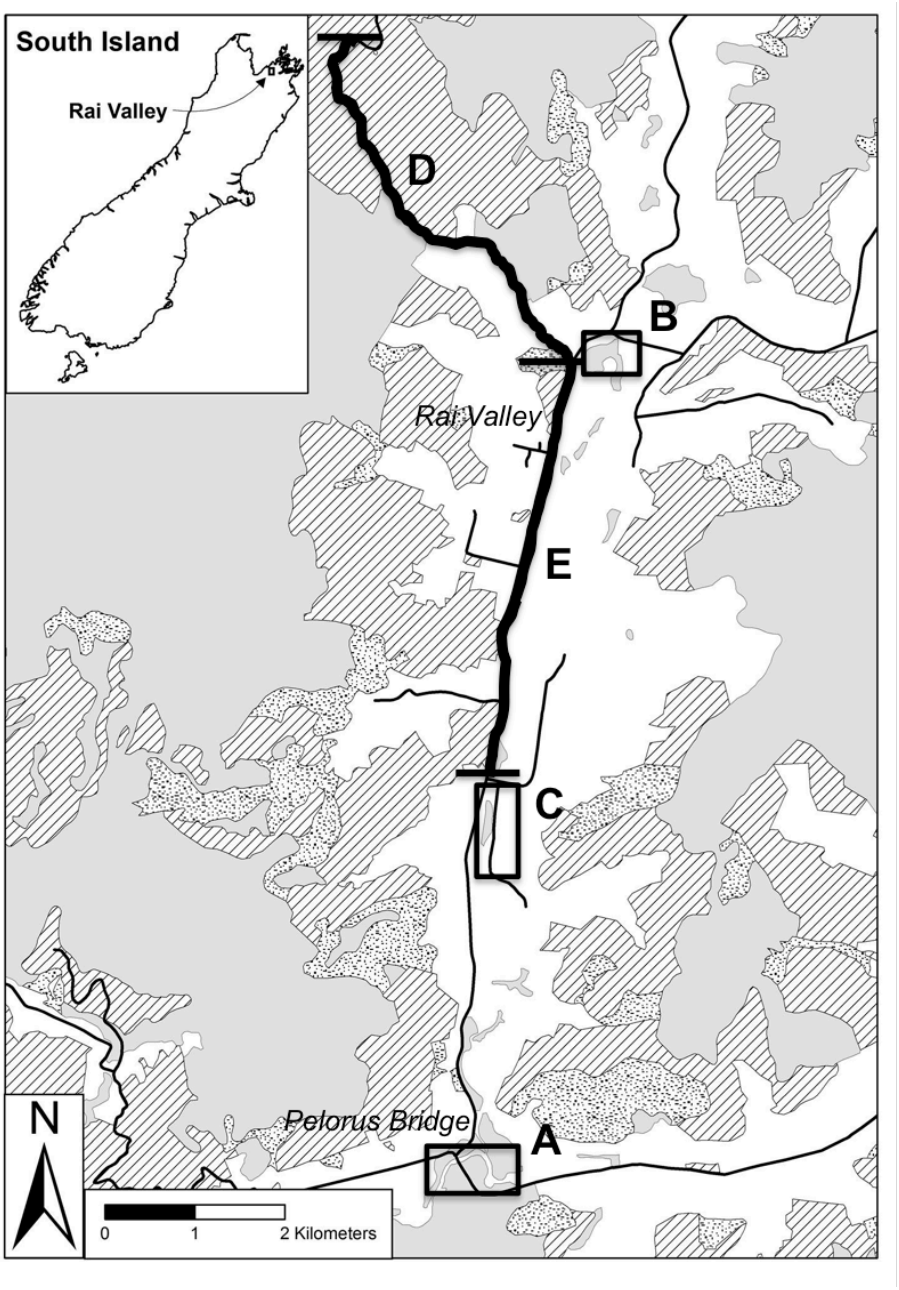


Figure 2.1. *Map of Rai Valley showing walking transect sites Pelorus Bridge (A), Carluke Reserve (B), Bulford (C), and road transects Rai Saddle (D) and Awakahakaha (E). Grey areas denote native forest, dotted areas denote native scrub, white areas denote cleared land, and thatched areas denote exotic forest.*

Driving counts were made from a vehicle moving at about 70 km per hour. This habitat was typically open farmland with a riparian strip of vegetation comprising mainly exotic deciduous species (willows and poplars), kōwhai, and beech alongside the Rai River (Fig. 1; transects D (Rai Saddle) and E (Awakahakaha)). Exotic plantation forestry

(*Pinus* spp.) occurred on both sides of the road along almost half of road transect A, and introduced broom (*Cytisus scoparius*) and the occasional wilding cherry (*Prunus avium*) grew along the roadside berm. The observer did not conduct habitat assessments at any of the sites, but there was no major change in habitat between the 1980s and 2000s. The observer also recorded casual observations of the food sources on which kererū were feeding and how conspicuous the birds were.

2.3.3 Seedfall counts

I analysed changes in the percentage of fruit handled by frugivores at Pelorus Bridge Scenic Reserve using a dataset of seedfall from Pelorus Bridge for six fleshy-fruited species - rimu, kahikatea, matai, miro, tawa, and hīnau. Strictly speaking, the Podocarpaceae produce reduced female cones with fleshy coverings or bases, but henceforth, for simplicity, I refer to all as fruits. All species produce single-seeded fruits so fruit number and seed number are interchangeable. Seedfall was monitored from 1986–1990 and 2004–2010. In 1986, seedfall traps were established beneath the canopies of reproductive adult trees (females for the podocarp species) of each of the six study species. Each species was allocated ten traps with the exception of rimu, which was allocated only five traps due to a shortage of reproductive female trees at the study site. Seedfall traps used from 1986 until 2009 were 0.10 m^2 cones suspended 1 m above ground; from 2010 these traps were replaced in the same locations by 0.28 m^2 cone traps suspended 1.2 m above the ground. Seed traps were opened on 1 January each year, then emptied on the first day of every month or second month over the fruiting season (January to October). The six species have overlapping fruiting phenologies at the site, with 78–95% of the annual seedfall being collected between January and May (Prado 2012). Samples were air-dried and fruits belonging to the study species were identified. These fruits were classed as either: handled by frugivores (clean seeds, with no fleshy pulp attached), damaged (with insect exit holes or mammal bite marks), or whole fruits found under parent trees. Very occasionally clean seeds also showed signs of predation; these fruits were not given their own classification due to how infrequently they occurred. Fruits handled by frugivores were easy to distinguish as they have a distinctive clean appearance with no flesh remaining on the seed, whereas fruits that have rotted or been preyed upon have some flesh

remaining on the seed or incisor marks. From 2004–2010 non-viable fruits (green, unripe fruits) and whole fruits falling away from parent trees were also recorded, but non-viable fruits were excluded from the analysis.

2.3.4 Statistical analysis

As there were only 7 years of overlapping kererū and seed trap data, I analysed trends in kererū counts and fruit handling rates separately. I examined changes in kererū abundance between the 1980s and 2000s by using the lme4 package (Bates et al. 2015) in R (R Core Team 2015) to generate a Poisson-distributed generalised linear mixed regression model (GLMM) with decade and month as fixed effects, and site as a random effect. Site referred to the five sites where counts were conducted (i.e. Rai Valley, Awakahakaha, Carlukes Reserve, Bulford, or Pelorus Bridge). Preliminary graphs depicted an August peak in kererū numbers, so months were converted to radians (with August = 0) and fitted with a cosine curve in the GLMM (i.e. cos[radians]) to test for seasonal changes in abundance (Stolwijk et al. 1999), using an interaction term between decade and cos[radians]. I added an observation level random effect to control for overdispersion (Browne et al. 2005). I also ran a generalised linear model (GLM) with a decade and cos[radians] interaction term and quasibinomial poisson family for the Pelorus Bridge kererū counts only, in order to assess changes in kererū detections at the same site as the seedfall counts. Lastly, I ran a GLM with decade as a predictor on the Pelorus Bridge kererū counts from January to June only, to determine whether kererū counts over the peak fruiting season changed between the two decades.

To analyse changes in dispersal quantity, I used the percentage of fruits that had been handled by birds out of the total fruit crop (i.e. handled by frugivores, whole, and damaged) for each species, summed across all traps (including those beneath other species) and all months to give an annual total. Whole fruit totals were underestimated from 1986–1990 due to whole fruits falling away from parent trees not being recorded, so I corrected these totals using proportions calculated from the 2004–2010 seed fall data. The proportions of whole fruits which were found in traps away from parent trees were 0.25 for hīnau, 0.05 for kahikatea, 0.22 for matai, 0.08

for miro, 0.96 for rimu, and 0.47 for tawa. Annual totals were classified as being either from the 1980s or 2000s. I used the lme4 package in R to generate a quasibinomial generalized linear model with the percentage of fruit handled by frugivores as a response, and decade as a predictor. I also calculated the percentage of fruits that had been handled by birds using data from seedfall traps under parent trees only, in order to allow comparisons with other sites that use the same metric.

2.4 Results

2.4.1 Kererū counts over time

Average numbers of kererū counted across all sites were 0.95 ± 1.7 (mean ±95% CI) birds per count for the 1980s and 0.25 ± 0.60 for the 2000s (Fig. 2.2). I found a significant interaction in our GLMM between decade and cos[months] (Z = -4.962, P = <0.0001), meaning that kererū counts significantly declined between the 1980s and 2000s due to a change in seasonal abundance (Fig. 2.2a). Considering only the Pelorus Bridge data, the GLM found that decade (T = 3.422, P = 0.0007) and cos[months] (T = 2.669, P = 0.008) were significant terms, but the decade:cos[months] interaction term was not (T = -1.640, P = 0.102). Therefore, kererū declined between the two decades within Pelorus Bridge, but any changes in the seasonal pattern of abundance were not large enough to be significant. When considering only the January to June counts at Pelorus Bridge, the GLM showed changes in abundance at that time of year between the 1980s and 2000s were not significant (T = -1.523, P = 0.13).

Casual observations of kererū diet and conspicuousness across both decades suggested that kererū detectability changed seasonally. In September, kererū switched from feeding on native foliage to feeding on the developing leaf buds of deciduous trees, particularly willow. Kererū were highly visible in the willows at this stage, but over the next two months as the willow leaves expanded, kererū became less visible within them, therefore decreasing detectability.

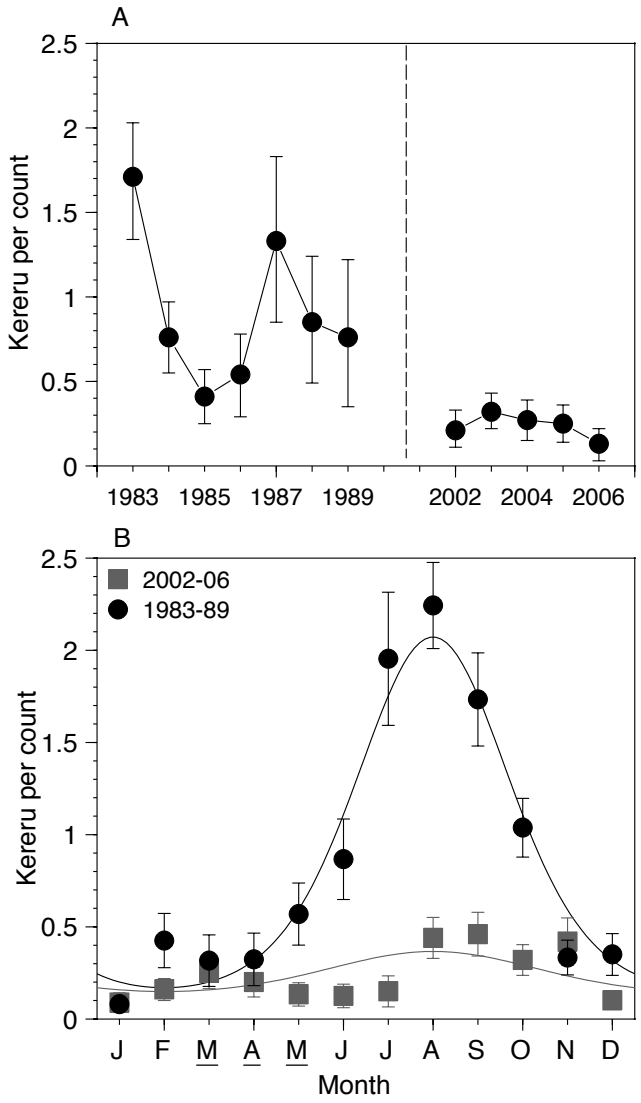


Figure 2.2 *Changes in kererū counts in the Pelorus area 1983–2006. (A) Annual mean kererū per count (±95% CI) on fixed transects in and around Pelorus Bridge, averaged across all months and sites. (B) Monthly counts (mean ±95% CI, with line showing GLMM fitted values) from 1983–89 and 2002–06. The austral autumn is March–May (underlined on X axis) and winter June–August. Kererū significantly declined between the two decades, mainly due to a decrease in July–September detections.*

2.4.2 Seed dispersal over time

Annual average fruit handling rates across all seedfall traps were high for kahikatea, rimu, and miro, but lower for tawa, matai, and especially hīnau (Table 2.1). Data from seedfall traps under parent trees only showed broadly similar results (Table 2.1).

Hīnau, rimu, and kahikatea fruit handling rates did not change significantly between the two decades (Fig. 2.3). Fruit handling rates of tawa increased significantly between the two decades (T = 3.134, P = 0.0139), while for matai rates decreased (T = -2.758, P = 0.0247).

Table 2.1. *Fruit handling rates for the six study species (for species names see Fig. 2.3) with total number of fruits trapped in 1986–1990 and 2004–2010. Average percentage of fruits handled by birds is from annual totals, both from all seedfall traps at the site (overall), and from seedfall traps under conspecific trees only.*

Species	Average % of fruits handled by frugivores (overall)	Average % of fruits handled by frugivores (under conspecific trees only)	Total number of fruits trapped
Kahikatea	72	74	44 278
Miro	52	39	876
Matai	23	20	4237
Hīnau	10	2	408
Tawa	24	7	305
Rimu	66	32	1069

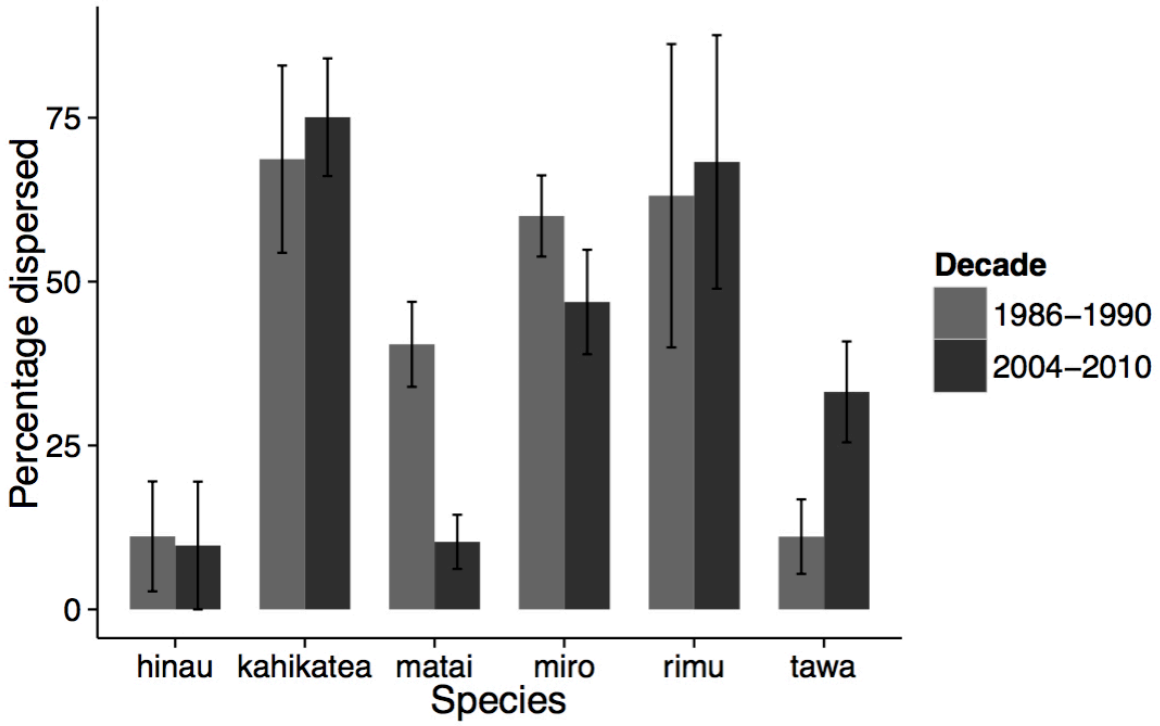


Figure 2.3. *Percentage of fruits handled by frugivores (mean ± SEM) per decade at Pelorus Bridge Scenic Reserve for the six study species (hīnau Elaeocarpus dentatus, kahikatea Dacrycarpus dacrydioides, matai Prumnopitys taxifolia, miro Prumnopitys ferruginea, rimu Dacrydium cupressinum, and tawa Beilshmiedia tawa).*

2.5 Discussion

2.5.1 Kererū

Kererū counts changed seasonally in both decades, with increased counts occurring in winter and early spring. However, winter kererū counts in the 2000s were much lower than winter kererū counts in the 1980s, resulting in a significant decline in overall kererū detections between the two decades. Kererū diet changes throughout the year, switching from primarily fruits from February to May to mainly foliage from June to January in the upper South Island (Clout et al. 1986). Accordingly, kererū move and choose their home ranges according to food source availability (Schotborgh 2005), so it seems likely that the high winter and early spring detections in the 1980s were driven by kererū moving into open river flats to feed on foliage. In addition, Clout et al. (1991) found that Pelorus Bridge Reserve harboured a resident population of kererū that

remained there year round, and a transient spring population that seasonally moved distances of up to 20 km. The seasonal increase in detections recorded in winter and early spring may have been due to non-resident kererū coming into the area, perhaps dispersing from native forests of Mount Richmond Forest Park in order to feed on spring foliage of willows and elms (*Ulmus* spp.) in the river valleys. Similarly, kererū counts at Lake Rotoroa (Nelson Lakes National Park) increased from June to September, when their diet switched from fruit to kowhai foliage on the lakeside (Clout et al. 1986). Kererū on Banks Peninsula have also been recorded occupying a circuit of seasonal home ranges (Schotborgh 2005). These findings show that kererū need to have access to either landscapes containing fragments of different habitat types, or large heterogeneous forest blocks, in order to meet their seasonally changing nutritional requirements (Emeny et al. 2009).

The observational data also suggest that kererū may have become more conspicuous in early spring due to feeding on leaf buds in willow trees with little foliage, increasing the detection rate. However, the count data show high kererū detections in the 1980s as early as July, which is too early to be explained by increased detectability while feeding on willow.

Therefore, it is unclear whether lower detections of kererū in late winter of the 2000s are due to changes in bird abundance or in bird habitat choice. Unfortunately, habitat assessments were not conducted at the site, so I do not know how resource availability and kererū detectability may have changed between the two decades. Although resources at the Pelorus Bridge site should not have changed, it is possible that trees were removed at the other sites, potentially depleting habitat quality – although the observer noticed no major changes to the habitat at any of the sites between the two decades. Likewise, habitat changes (such as increased food availability) may have occurred at sites that were not measured by our study, resulting in kererū moving to these unmeasured sites to feed in winter and early spring. Conversely, the data may document a genuine decline in kererū abundances. Given that Clout et al. (1995) found that the Pelorus Bridge kererū population was vulnerable to decline due to high rates of mammalian predation and low breeding success, that result would be unsurprising. Mammalian predator control was commenced at Pelorus Bridge Scenic Reserve in

2010, which may have possibly improved kererū numbers after the observer stopped counting them. Studies of long-term trends in other kererū populations would be valuable, in order to assess how prevalent are declines.

My study also highlights the difficulty of monitoring kererū, due to their crypsis, seasonally mobile behaviour, and highly variable detectability. While five-minute bird counts have been the most commonly used method for monitoring diurnal birds in New Zealand since the 1970s, kererū are typically quiet and sedentary, so numbers detected per five-minute count are generally low. As a result, such counts lack the sensitivity to detect 20–30% changes in kererū abundances in very small forest patches (Mander et al. 1998). Distance sampling appears to be a better method, as it allows calculation of the effective sampling area in different habitats, and can theoretically control for differences in detectability with increasing distance from the observer (Mander et al. 1998). However, distance sampling assumes detectability directly overhead is 100% so is still affected by the general crypsis of kererū. Census counts from vantage points give a minimum estimate of the actual number of kererū using the observed area for small forest fragments, but are labour intensive and would not be as effective where the terrain is flat or where there are more than 20 birds present (Mander et al. 1998). The high degree of seasonal mobility recorded within the Rai Valley population suggests that monitoring at several times throughout the year would be optimal.

2.5.2 Fruit-handling and dispersal

Despite an overall reduction in kererū detections, fruit-handling rates at Pelorus did not worsen overall between the 1980s and 2000s. While fruit handling rates do not explicitly measure quantitative seed dispersal (as successful seed dispersal typically requires the movement of fruits away from beneath parent tree canopies), they are monotonically related to the percentage of seeds that are moved away from beneath the parent canopy and therefore they can function as an index of dispersal quantity (Wyman 2013). Additionally, some of the frugivore-handled fruits recorded in this study were found in traps away from parent trees and therefore were successfully dispersed. Seed dispersal at Pelorus probably did not worsen between the two

decades due to the fact that 85% of the seed crop from the six fleshy-fruited trees falls between January and May, during which time period kererū at Pelorus Bridge were at similar densities over the two decades. Additionally, other bird species are likely to have been important seed dispersers for smaller-seeded tree species such as kahikatea (O'Donnell and Dilks 1994). Bellbirds, tūī, and silvereyes are thought to be present in the reserve (Robertson et al. 2007) and are capable of making significant contributions to seed dispersal (Kelly et al. 2006). It is important to also note that while brushtail possums (*Trichosurus vulpecula*) are typically thought of as seed predators, they have also been recorded dispersing fruit, and therefore may be facilitating seed dispersal at Pelorus at least for smaller-seeded species (Williams et al. 2000). Tawa, miro, and hīnau are the three species that are probably now dispersed predominantly by kererū, but none of these species' dispersal declined between the two decades (also see Pegman 2012).

There is no objective definition of what constitutes 'good' or 'poor' dispersal quantity, so it is difficult to say whether or not the levels of dispersal quantity at Pelorus Bridge were adequate (Kelly et al. 2010). Although there are few published data, dispersal quantity at Pelorus Bridge was generally lower than at other sites in New Zealand. Over nine seasons at Blue Duck Scientific Reserve, near Kaikoura, an average of 50% of tawa seeds underneath parent trees had been handled by frugivores (Kelly et al. 2010), compared to an average of 7% at Pelorus. Unpublished seedfall data (JK Carpenter, unpubl. data) from Blue Duck, Waipapa, Otamatuna, Trounson and Paengaroa over 3 to 4 years found average dispersal quantities under parent trees of 67% for kahikatea, 65% for matai, 51% for miro, 62% for rimu, and 28% for hīnau. Therefore, with the exception of kahikatea, Pelorus Bridge has lower average dispersal quantities than these sites, although the averages from the other sites may be skewed by the small number of seasons over which seedfall was collected.

When the trap data from non-parent trees are included, the species measured at Pelorus Bridge probably have adequate dispersal, with the exception of hīnau and perhaps matai. Hīnau fruits have a conspicuous metallic sheen and are dropped at maturity, prompting Lord et al. (2002) and Thorsen et al. (2011) to speculate that they may have evolved to be dispersed by flightless birds. The only extant species that have

been recorded consuming hīnau are kererū, weka (*Gallirallus australis*), kōkako (*Callaeus cinerea*), and brown kiwi (*Apteryx mantelli*) (Kelly et al. 2010), of which the latter three are severely range restricted. Low dispersal quantities for matai are more puzzling. O'Connor (2012) recorded dispersal quantities of between 19 and 55% under matai parent trees in fragmented forest on Banks Peninsula, prompting her to speculate that matai might be an important resource for frugivorous birds in that highly modified habitat. Pelorus Bridge contains several other fleshy-fruited species, so matai may not be such an important food source and hence suffer from lower dispersal quantity at the site.

In conclusion, the results presented here illustrate the value of long-term studies to reveal potential changes in ecological services such as seed dispersal. They also highlight the importance of considering seasonality when monitoring trends in frugivore abundances and seed dispersal.

2.6 References

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48 . doi: 10.18637/jss.v067.i01

Boyer AG (2010) Consistent ecological selectivity through time in Pacific Island avian extinctions. Conserv Biol 24:511–519 . doi: 10.1111/j.1523-1739.2009.01341.x

Browne WJ, Subramanian S V., Jones K, Goldstein H (2005) Variance partitioning in multilevel logistic models that exhibit overdispersion. J R Stat Soc Ser A Stat Soc 168:599–613 . doi: 10.1111/j.1467-985X.2004.00365.x

Bull PC, Gaze PD, Robertson CJR (1985) The Atlas of Bird Distribution in New Zealand. Ornithological Society of New Zealand.

Burrows C. (1994) Fruit, seeds, birds and the forests of Banks Peninsula. New Zeal Nat Sci 21:87–108

Clout MN, Gaze PD, Hay JR, Karl BJ (1986) Habitat use and spring movements of New Zealand pigeons at Lake Rotoroa, Nelson Lakes National Park, New Zealand. Notornis 33:37–44

Clout MN, Hay JR (1989) The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. N Z J Ecol 27–33 . doi: 10.2307/24053245

Clout MN, Karl BJ, Gaze PD (1991) Seasonal movements of New Zealand pigeons from a lowland forest reserve. Notornis 38:37–47 . doi: 10.1111/j.1365-2486.2006.01193.x

Clout MN, Karl BJ, Pierce RJ, Robertson HA (1995) Breeding and survival of New Zealand Pigeons Hemiphaga novaeseelandiae. Ibis (Lond 1859) 137:264–271 . doi: 10.1111/j.1474-919X.1995.tb03248.x

Clout MN, Tilley JA V, Clout NN (1992) Germination of miro (Prumnopitys ferruginea) seeds after consumption by New Zealand pigeons (Hemiphaga novaeseelandiae). New Zeal J Bot 30:25–28 . doi: 10.1080/0028825X.1992.10412882org/10.1080/0028825X.1992.10412882

Emeny MT, Powlesland RG, Henderson IM, Fordham RA (2009) Feeding ecology of kereru (Hemiphaga novaeseelandiae) in podocarp-hardwood forest, Whirinaki Forest Park, New Zealand. N Z J Ecol 33:114–124

Iles JM (2012) Is Maungatautari restoring bird pollination and seed dispersal services? University of Canterbury

Kelly D, Ladley JJ, Robertson AW, et al (2010) Mutualisms with the wreckage of an

avifauna: the status of bird pollination and fruit- dispersal in New Zealand. N Z J Ecol 34:66–85

Kelly D, Robertson AW, Ladley JJ, et al (2006) Relative (un)importance of introduced animals as pollinators and dispersers of native plants. In: Biological Invasions in New Zealand. pp 227–245

Lord J (2002) Have frugivores influenced the evolution of fruit traits in New Zealand? In: DJ L, WR S, M G (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, WallingfoRd, UK, pp 55–68

Mander C, Hay R, Powlesland R (1998) Monitoring and management of kereru (Hemiphaga novaeseelandiae)

McEwen WM (1978) The food of the New Zealand pigeon (Hemiphaga novaeseelandiae novaeseelandiae). N Z J Ecol 1:99–108 . doi: 10.1002/jid

McNutt KL (1998) Impacts of reduced bird densities on pollination and dispersal mutualisms in New Zealand forests. Massey University, New Zealand

Miskelly CM, Dowding JE, Elliott GP, et al (2008) Conservation status of New Zealand birds, 2008. Notornis 55:117–135

O'Connor S-J (2012) Quantifying seed dispersal of matai (Prumnopitys taxifolia)

O'Donnell CFJ, Dilks PJ (1994) Foods and foraging of forest birds in temperate rainforest, , South Westland, New Zealand. N Z J Ecol 18:87–107 . doi: 10.1093/iis/etq042

Pegman APMcK (2012) Reconstruction of seed dispersal via modeling, seedling recruitment, and dispersal efficiency of Hemiphaga novaeseelandiae in Vitex lucens and Prumnopitys ferruginea in New Zealand. University of Auckland

Pierce RJ, Graham PJ (1995) Ecology and breeding biology of kukupa (Hemiphaga novaeseelandiae) in Northland. Wellington, Department of Conservation.

Prado RCJ (2012) Animal seed dispersal and its consequences for plant recruitment. University of Canterbury.

Robertson AW, Ladley JJ, Kelly D, et al (2008) Assessing pollination and fruit dispersal in Fuchsia excorticata (Onagraceae). New Zeal J Bot 46:299–314 . doi: 10.1080/00288250809509768

Robertson C, Hyvőnen P, Fraser MJ, Pickard CR (2007) Atlas of Bird Distribution in New Zealand 1999-2004. Ornithological Society of New Zealand

Schotborgh HM (2005) An analysis of home ranges, movements, foods, and breeding of kereru (Hemiphaga novaeseelandiae) in a rural-urban landscape on Banks Peninsula,

New Zealand. Lincoln University

Sekercioglu CH, Daily GC, Ehrlich PR (2004) Ecosystem consequences of bird declines. Proc Natl Acad Sci 101:18042–18047 . doi: 10.1073/pnas.0408049101

Stolwijk AM, Straatman H, Zielhuis GA (1999) Studying seasonality by using sine and cosine functions in regression analysis. J Epidemiol Community Health 53:235–238 . doi: 10.1136/jech.53.4.235

Thorsen MJ, Seddon PJ, Dickinson KJM (2011) Faunal influences on New Zealand seed dispersal characteristics. Evol Ecol 25:1397–1426 . doi: 10.1007/s10682-011-9470-1

Williams PA, Karl BJ, Bannister P, Lee WG (2000) Small mammals as potential seed dispersers in New Zealand. Austral Ecol 25:523–532 . doi: 10.1046/j.1442-9993.2000.01078.x

Wotton DM, Kelly D (2011) Frugivore loss limits recruitment of large-seeded trees. Proc R Soc B Biol Sci 278:3345–3354 . doi: 10.1098/rspb.2011.0185

Wyman TE (2013) Consequences of reduced bird densities for seed dispersal. University of Canterbury

UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

Deputy Vice-Chancellor's Office
Postgraduate Research Office

Co-Authorship Form

This form is to accompany the submission of any thesis that contains research reported in co-authored work that has been published, accepted for publication, or submitted for publication. A copy of this form should be included for each co-authored work that is included in the thesis. Completed forms should be included at the front (after the thesis abstract) of each copy of the thesis submitted for examination and library deposit.

Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter 3; published in Proceedings of the Royal Society B: Biological Sciences

Carpenter JK, Wood JR, Wilmshurst JM, Kelly D. 2018. "An avian seed dispersal paradox: New Zealand's extinct megafaunal birds did not disperse large seeds." Proceedings of the Royal Society B 285 (1877), 20180352.

Please detail the nature and extent (%) of contribution by the candidate:

Jo Carpenter developed the study questions, collected new data (seed compression measurements), analysed all the data, created graphs, and wrote the manuscript (70%).

Certification by Co-authors:

If there is more than one co-author then a single co-author can sign on behalf of all

The undersigned certifies that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name: Dave Kelly Signature: Dave Kelly Date: *6/2/2019*

3

An avian seed dispersal paradox: New Zealand's extinct megafaunal birds did not disperse large seeds

Moa coprolite. The pale objects are Coprosma seeds. Credit: Jamie Wood

3.1 Abstract

Often the mutualistic roles of extinct species are inferred based on plausible assumptions, but sometimes palaeoecological evidence can overturn such inferences. I present an example from New Zealand, where it has been widely assumed that some of the largest-seeded plants were dispersed by the giant extinct herbivorous moa (Dinornithiformes). The presence of large seeds in preserved moa gizzard contents supported this hypothesis, and five slow-germinating plant species (*Elaeocarpus dentatus, E. hookerianus, Prumnopitys ferruginea, P. taxifolia, Vitex lucens*) with thick seedcoats prompted speculation about whether these plants were adapted for moa dispersal. However, I demonstrate that all these assumptions are incorrect. While large seeds were present in 48% of moa gizzards analysed, analysis of 152 moa coprolites (subfossil faeces) revealed a very fine-grained consistency unparalleled in extant herbivores, with no intact seeds larger than 3.3 mm diameter. Secondly, prolonged experimental mechanical scarification of *E. dentatus* or *P. ferruginea* seeds did not reduce time to germination, providing no experimental support for the hypothesis that present-day slow germination results from the loss of scarification in moa guts. Paradoxically, although moa were New Zealand's largest native herbivores, the only seeds to survive moa-gut passage intact were those of small seeded herbs and shrubs.

3.2 Introduction

The last 50,000 years have seen the widespread extinction of large herbivores globally (Johnson 2009). North and South America lost around 84 megafaunal genera at the end of the Pleistocene, while Australia lost 14 of its large herbivore genera around 30,000 years earlier (Koch and Barnosky 2006; Gillespie et al. 2012; Mcdowell et al. 2015). Understanding the ecological consequences of these extinctions is important when evaluating current ecosystem functioning, but the ecosystem services provided by many of these lost species, and the legacy of their losses, are still unclear (Johnson 2009; Lee et al. 2010; Wood and Wilmshurst 2017; Otto et al. 2017).

Seed dispersal is a mutualism that has been studied in some depth for extinct fauna (Galetti et al. 2017; Pires et al. 2018), but detailed data on the quality and quantity of the dispersal services provided by extinct species are rare. Consequently, the traits of dispersed fruits and the quality of dispersal service provided by extinct megafauna are usually inferred based on plausible assumptions. As a strong correlation exists between fruit size and disperser size (Burns 2013; Federman et al. 2016), one of the most common assumptions is that extinct megafaunal frugivores consumed and dispersed the largest fruits. For example, Janzen and Martin (Janzen and Martin 1982) proposed that extinct Central American megafauna had a central role in the dispersal and evolution of several large angiosperm seeds. Their argument was supported by the existence of dispersal anachronisms – plant species with seed traits (such as size) that appear maladapted for dispersal by the contemporary fauna, haunted by the "ghosts of past mutualisms" (Barlow 2002). As well as being large seeded, these putatively anachronistic plants had fruits that dropped to the ground when ripe (early abscission), where the terrestrial megafauna could access them; were unattractive to arboreal or volant frugivores; showed low contemporary dispersal rates; and had seeds that were protected by a thick, woody, endocarp (Janzen and Martin 1982). Since Janzen and Martin first proposed their hypothesis for Central America, other putative anachronistic seeds with extinct dispersers have been recognised, involving the giant Malagasy elephant birds (*Aepyornis*) (Midgley and Illing 2009), giant tortoises in Mauritius (Griffiths et al. 2011), and Australian mihirungs (*Dromornis*) (Murray and

Vickers-Rich 2004), among others (Galetti et al. 2017). The majority of these hypotheses are underpinned by the assumption that the largest extinct herbivores were dispersers of the largest seeds, but thus far fossil evidence has been insufficient to test whether this assumption actually holds true, although there have been some indications of its limitations (e.g. Chen and Moles 2015; Baños-Villalba et al. 2017). These limitations are of concern if they result in the erroneous identification of 'gaps' in seed dispersal networks. For example, the Amazonian motacú palm (*Attalea princeps*) conforms exactly to the classic megafaunal fruit syndrome outlined by Guimarães et al. (fleshy fruits 4-10 cm diameter with up to five seeds), but is actually being effectively dispersed by several species of macaw (*Ara spp.*), despite the macaws' comparatively small size (Guimarães et al. 2008; Baños-Villalba et al. 2017).

New Zealand offers an ideal case study to test the validity of the assumption that large extinct frugivores were important dispersers of large-seeded, putatively anachronistic plants. The extinct moa of New Zealand (Aves: Dinornithiformes) were nine species (Bunce et al. 2009) of flightless herbivorous ratites. With body masses ranging from 15 to >200 kg (Worthy and Holdaway 2002), they were the largest terrestrial herbivores in New Zealand's prehistoric ecosystems before their extinction, driven by human hunting, ~500 years ago (Perry et al. 2014). They went extinct so recently that there is a rich subfossil record, including bones, skins, eggshell and coprolites (mummified faeces) (e.g. Wood et al. 2008; Huynen et al. 2010; Rawlence et al. 2013; Perry et al. 2014), allowing an unusually comprehensive analysis of the ecosystem services these birds provided (Wood et al. 2013a).

Since the discovery of several subfossil moa gizzards containing large seeds (Clout and Hay 1989; Lee et al. 1991; Kelly et al. 2010; Thorsen et al. 2011), moa have been widely proposed as dispersers of large, thick-endocarp-protected seeds. Clout and Hay (1989) suggested that the giant New Zealand ratites might have performed a similar role to that of their extant relative the cassowary (*Casuarius* spp.), which consumes and disperses large amounts of large fallen fruit in tropical forests of Northern Australia, New Guinea, and Yapen (Stocker and Irvine 1983; Westcott et al. 2005). Although the New Zealand flora lacks species with fruits large enough to fit the classic megafaunal fruit syndrome (New Zealand mean fruit diameters $\leq$23 mm: (Lord 2002; Guimarães et

al. 2008; Kelly et al. 2010)), five endemic plant species with early abscission and unusually thick-walled (2-3 mm) endocarps have been suggested as being adapted for dispersal by moa: *Elaeocarpus dentatus, E. hookerianus* (Elaeocarpaceae), *Prumnopitys ferruginea, P. taxifolia* (Podocarpaceae), and *Vitex lucens* (Labiatae) (Fig. 3.1; Kelly et al. 2010). All these species have moderate to large fruits by New Zealand standards (*V. lucens* 15 mm mean fruit diameter, *P. ferruginea* 13 mm, *E. dentatus* and *P. taxifolia* 9.4 mm, *E. hookerianus* 7.2 mm (Lord 2002; Kelly et al. 2010); for further descriptions of these fruits see Appendix 3.1). The slow germination (2 – 7 years) currently experienced by four of these species (all except *P. taxifolia*) prompted speculations that these seeds were adapted to survive passage through a stone-filled moa gizzard, with the abrasion thinning the seedcoat and perhaps hastening germination times (Clout and Hay 1989; Kelly et al. 2010).

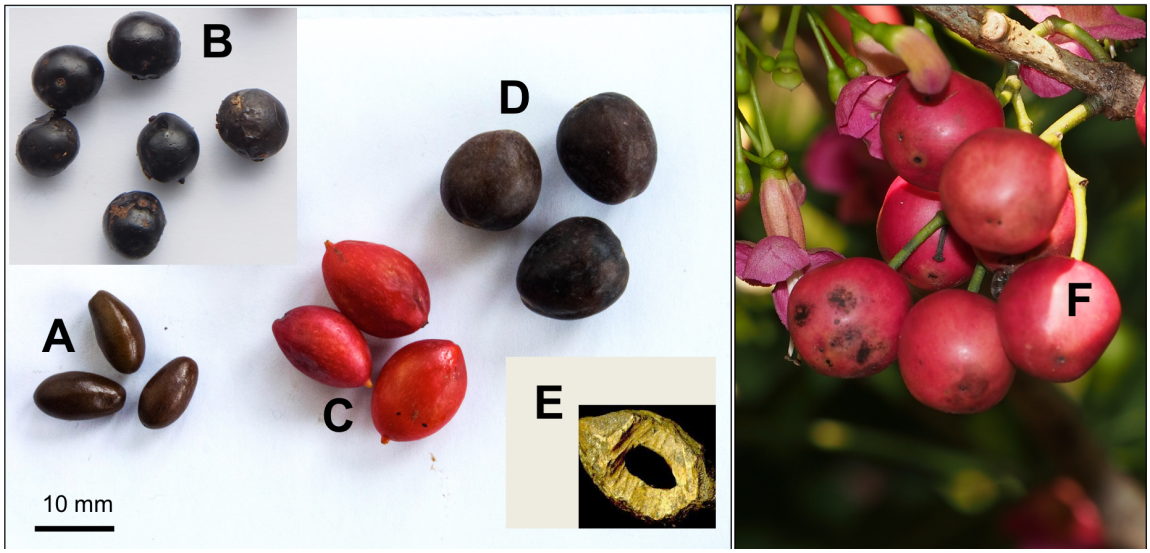


Figure 3.1. *New Zealand's five species of putative moa-dispersed fruit. A) Elaeocarpus hookerianus; B) Prumnopitys taxifolia; C) Prumnopitys ferruginea; D) Elaeocarpus dentatus; E) detail showing woody endocarp of Prumnopitys ferruginea seed; F) Vitex lucens.*

Over the past decade, new insights into the role that these birds played in pre-human New Zealand have come from analyses of more than 150 subfossil moa coprolites (Wood et al. 2008, 2012a, 2013a, Wood and Wilmshurst 2014, 2017). This large sample size provides the basis for my quantitative examination of the role of moa as dispersers of large, endocarp-protected seeds. Coprolites are particularly useful for

studying seed dispersal as they represent the post-digestion stage and the potential for dispersal, unlike gizzards, the contents of which can only demonstrate consumption. This distinction is especially important when studying birds with stone-filled gizzards, where the grinding action of the muscular gizzard may destroy many seeds (Soons et al. 2008; Fritz et al. 2011).

I analysed published macrofossil and ancient DNA (aDNA) data from 23 preserved gizzards and 152 coprolites, recovered from thirteen sites spanning the South Island of New Zealand (Fig. 3.2), to determine whether moa ate and dispersed large seeds. I also tested whether prolonged mechanical scarification (used to simulate moa gut passage) of putatively moa-dispersed endocarps of *E. dentatus* and *P. ferruginea* decreased their time to germination. As I was interested in the protection conferred by the woody endocarps of the putative moa-dispersed plant species, I also tested the mechanical force needed to crush *E. dentatus* endocarps.

3.3 Methods

3.3.1 Dataset of seeds in coprolites and gizzards

Gizzards were obtained from four sites in the South Island (Cheviot, Pyramid Valley, Scaifes Lagoon, Styx Mire; Fig. 3.2), and sampled four moa species (*Dinornis robustus, Emeus crassus, Euryapteryx curtus, Pachyornis elephantopus*).

Coprolites were obtained from nine South Island sites (Takahe Valley, Sawers rockshelter, Roxburgh Gorge, Old Man Range, Mount Nicholas, Kawarau Gorge, Euphrates Cave, Earnscleugh Cave, Dart River; Fig. 3.2). The coprolites sampled three of the species represented by gizzard fossils (*D. robustus, E. curtus, P. elephantopus*) plus two others (*Anomalopteryx didifornis, Megalapteryx didinus*) for a total of five moa species.

I used a dataset of all seeds found in these coprolites and gizzards from Falla (1941), Burrows et al. (1980), Horrocks et al. (2004), Wood (2007), and Wood et al. (2008, 2012b, a, 2013a; Wood and Wilmshurst 2014). I also noted *Prumnopitys* and *Elaeocarpus* pollen and aDNA records for each sample (where tested) as evidence that

these genera were growing locally or in the diet. There were no data on the presence of *Prumnopitys* aDNA in coprolites as the PCR primers used do not amplify conifer DNA. Presence of *Prumnopitys* or *Elaeocarpus* at the sites was indicated by the presence of the taxon's pollen, macrofossils or aDNA in the fossils, or from the presence of macrofossils recovered from the surrounding soil layer.

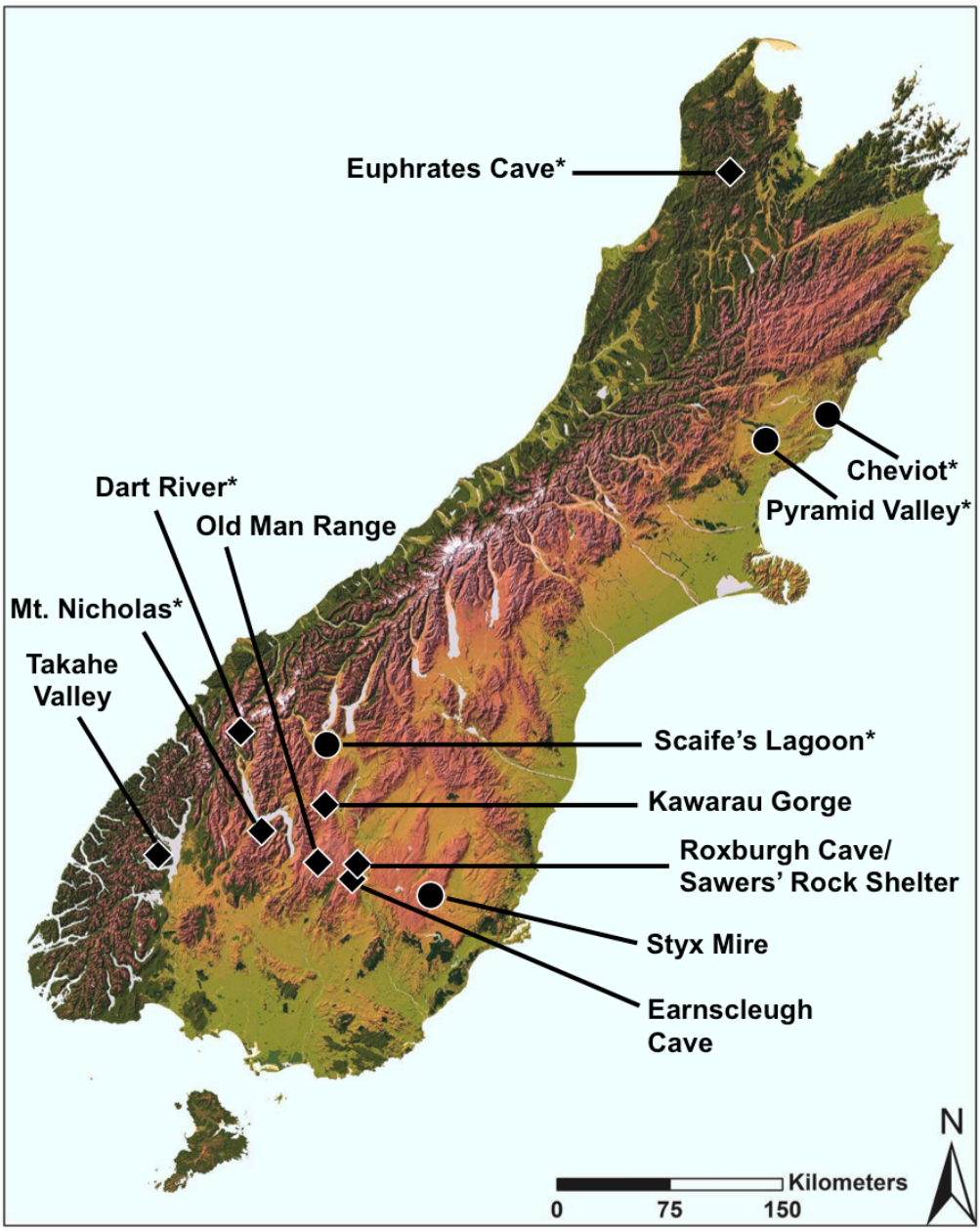


Figure 3.2. *The South Island of New Zealand, showing sites where analysed coprolites (diamonds) and gizzards (circles) were recovered. The * symbol denotes sites where Prumnopitys or Elaeocarpus were also indicated to be present, based on pollen records, aDNA, and macrofossils. GIS layer from www.geographx.co.nz*

3.3.2 Seed size in coprolites and gizzards

I used published records (Moore and Edgar 1970; Webb and Simpson 2001) to obtain mean seed lengths for each plant species with seeds detected in gizzards and coprolites. I used length rather than diameter as I was interested in the largest dimension of the seeds, but for New Zealand fruits (and seeds) under 10 mm diameter, length and diameter are similar (Lord 2002). Some seeds in the samples were only identified to genus level; these were given a mean length based on other identified species of that genus found in moa coprolites or gizzards. If no other species of that genus occurred within the fossils, the genus was generally given the mean of all native species within that genus. For *Carex* I used the mean of twenty randomly selected *Carex* species, due to the large number of native species in the genus. Seeds from a coprolite recovered from Earnscleugh Cave that were only identified as '*Veronica*' were given the mean of thirteen *Veronica* (previously *Hebe*) species that occurred in the region where the fossil was recovered. Species that were identified to above the genus level, or were identified to the genus level but only had one seed counted across all the fossils, were not included in the analysis (172 seeds). Analysis was conducted on a total of 9039 seeds. The number of seeds in a single *Euryapteryx curtus* gizzard was not described so this sample was not included in this analysis.

3.3.3 Germination experiments on the putative moa dispersed seeds

Dave Kelly and Jenny Ladley commenced germination experiments in August 2009. They subjected *P. ferruginea* and *E. dentatus* seeds collected in Blue Duck reserve, Kaikoura (42° 14' S, 173° 47' E) in August 2009 to five different scarification treatments to test whether treatments altered time to germination. The five scarification treatments were (1) 30 minutes mechanical scarification, (2) 4 hours mechanical scarification, (3) 30 minutes mechanical scarification plus acid scarification, (4) 4 hours mechanical scarification plus acid scarification, and (5) acid scarification only (*E. dentatus* only). Mechanically-scarified seeds were placed in a motorised portable concrete mixer with 2 litres of water and 2 litres of gravel chips (2 – 4 cm in length), where they were tumbled for either 30 minutes or 4 hours. Acid-scarified seeds were placed on a tray (post-mechanical scarification, if relevant), covered with 0.5%

hydrochloric acid, and held for 48 hours at 38° C to crudely represent gut passage acidity and temperature. Sample sizes for each treatment ranged from 50 – 100 seeds for each species. The time to germination of treated seeds was compared to the time to germination for whole seeds (*E. dentatus* only) and seeds that had been processed in a way that mimics an extant frugivorous bird's gut passage ('hand-cleaned'; (Robertson et al. 2006)). Hand-cleaned seeds were rubbed by hand until the fleshy exocarp was removed. All whole seeds and 100 hand-cleaned seeds of *E. dentatus* were cold stratified at 1.6° C for 8 weeks prior to sowing, in case cold stratification was needed to break seed dormancy. The seeds from each treatment were planted in potting mix in one seed tray each and kept in an unheated shadehouse, where they were watered once daily. Trays were checked three times a year for seedling emergence for five years after sowing. Seven years after sowing trays were checked again and new seedlings were aged by size and bud scars to determine whether they germinated in years 6 or 7.

3.3.4 Endocarp strength tests

I tested the force needed to rupture 14 fresh *Elaeocarpus dentatus* endocarps using a MTS Criterion Model 43 with a 2.5kN cell and a crosshead speed of 5mm/min. Fresh *E. dentatus* fruits were collected from the ground beneath a tree at the University of Canterbury, Christchurch, and were tested without additional drying. Seeds were oriented with their sutures vertical to the loading direction and their shorter dimension parallel to the loading direction, following the method of Schüler et al. (Schüler et al. 2014).

3.3.5 Statistical analysis

All analyses were performed in R version 3.3.0. I used a Fishers Exact Test to test whether there was a significant difference between the proportion of gizzards and coprolites that contained seeds of *Elaeocarpus dentatus, E. hookerianus, Prumnopitys ferruginea,* or *P. taxifolia*. Only subfossils that were recovered from sites where either *Prumnopitys* or *Elaeocarpus* were indicated to be present were included in this analysis. I did not test for the presence of *Vitex lucens* as it is native to only the North Island of New Zealand, whereas moa gizzard and coprolite samples have only been

found in the South Island. The assumption of independence was potentially violated as some of the coprolites may have been produced by the same individual bird, but the large number of coprolites obtained from multiple different sites reduces this risk.

I used the *lme4* package (Bates et al. 2015) to perform a linear mixed effects analysis on the length of seeds found in the two subfossil types to test whether coprolites had significantly smaller seeds than gizzards. Seed lengths were log transformed to improve normality. I used subfossil type as a fixed effect, and sample nested within site as random effects. Moa species was not included as an effect because species identity was not known for some coprolites and gizzards. P-values were obtained by likelihood ratio tests of the full model with a fixed effect for subfossil type against the model without the fixed effect for subfossil type.

I used Cox Proportional Hazard (CPH) regression models to test whether the scarification treatments decreased the germination time for seeds of *E. dentatus* and *P. ferruginea* that germinated within 7.2 years (McNair et al. 2012). I fitted CPH models to data consisting of the number of years between initiation of germination trials and seedling emergence, for each individual seed. Only data from seeds that germinated by the end of the study were included to separate the effects of treatment on the rate of germination from the effects on final germination percentages ((Robertson et al. 2006); see Figuerola et al. (2010) for a similar approach). I used the 'survival' package in R to fit the models. Schoenfeld tests were conducted to confirm the assumption of proportionate hazards. I also tested for differences between the final percentages of germinated seeds after 7.2 years for the two plant species. I grouped treatments as mechanically scarified, hand-cleaned, or whole seeds (*E. dentatus* only) and tested for differences between them using a Chi-squared test. I used the 'fifer' package in R to run post-hoc tests with a false discovery rate adjustment for multiple comparisons. All germination treatments which included acid scarification gave extremely low numbers of germinated seeds, so those treatments were excluded from all analyses.

3.4 Results

3.4.1 Presence of putative moa-adapted seeds in coprolites and gizzards

None of the gizzards or coprolites came from the North Island where *Vitex* occurred (Fig. 3.2), but moa ate fruits of *Prumnopitys taxifolia* and *Elaeocarpus hookerianus*. Moa coprolites were found to have a very finely ground texture with no large seeds present, with a consistency more similar to the droppings of ruminant mammals than extant ratites. Although particle size was not measured, the fine grained consistency is clear in comparative photos (Fig. 3.3). There was a significant difference between the proportion of gizzards and coprolites that contained the woody endocarp-protected seeds (hereafter just referred to as 'seeds') of *Elaeocarpus dentatus, E. hookerianus, Prumnopitys ferruginea,* or *P. taxifolia.* Almost half (48%) of the 23 gizzards contained identifiable remains of either *P. taxifolia* or *E. hookerianus* seeds, and 17% contained both. None of the 152 coprolites contained any intact *Prumnopitys* or *Elaeocarpus* seeds, or identifiable remains of these seeds, ($P < 0.001$; Fishers Exact Chi-sq Test), despite the fact that 82.9% of the coprolites were recovered from sites where *Prumnopitys* or *Elaeocarpus* were present, based on pollen, macrofossil, or aDNA evidence (Appendix 3.2). *Elaeocarpus* aDNA was present in 27% of coprolites that had been analysed for aDNA (n = 30), and a further 23% contained Oxalidales aDNA (the order that contains *Elaeocarpus*), although this aDNA could have come from foliage as well as pulverised seeds. The abundance of small seeds that ripen in summer or autumn (e.g. *Fuchsia excorticata*, *Gaultheria* spp.) in these coprolites indicated that many of the coprolites were deposited when fruits of *Elaeocarpus* and *Prumnopitys* would have been available (Webb and Simpson 2001). Taken together, these data suggest that *Elaeocarpus* and *Prumnopitys* fruit were being eaten by moa, but did not survive gut passage intact. Wood et al. (2008) recorded several gymnosperm and podocarp seed fragments in coprolites that could have come from *Prumnopitys*, although none of the fragments could be identified microscopically to the species level. Many small seeds discovered in coprolites were also broken.

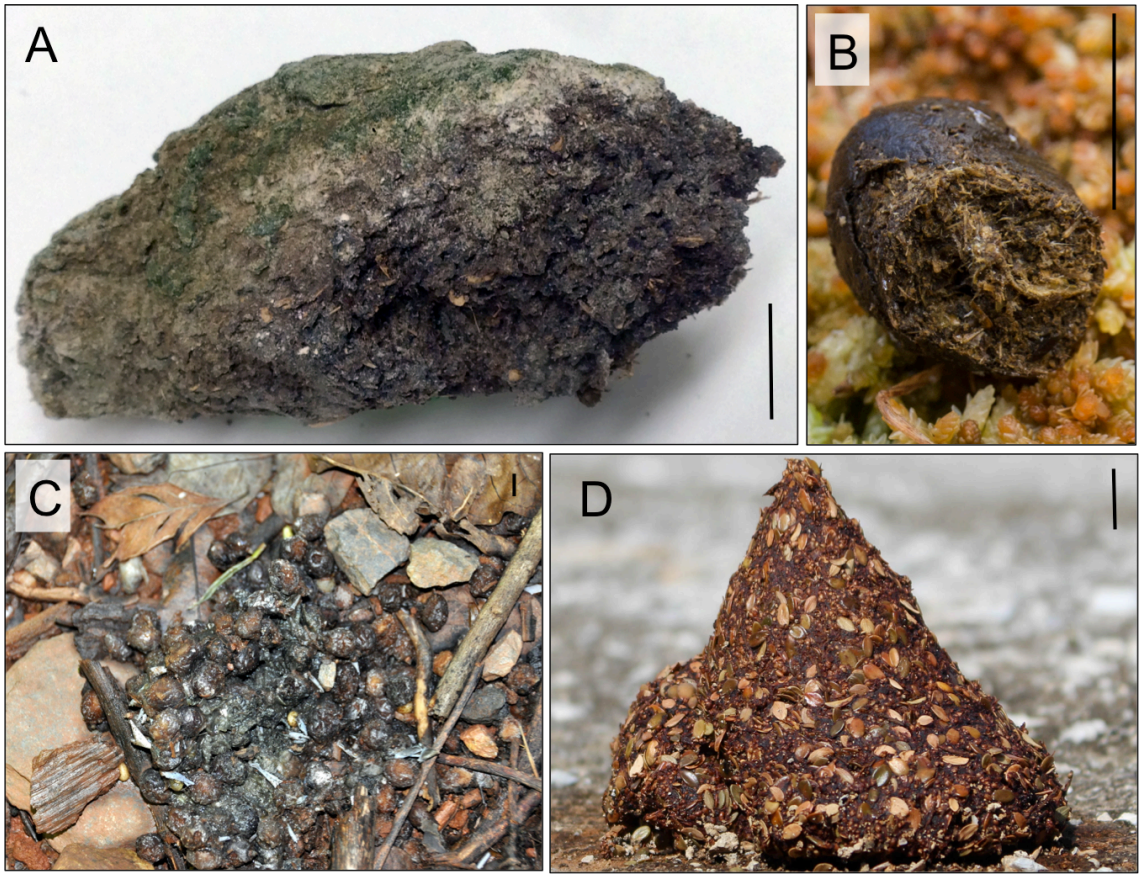


Figure 3.3. *Photos showing the consistency of faecal deposits from (A) moa, (B) red deer Cervus elaphus, (C) cassowary Casuarius sp., and (D) emu Dromaius novaehollandiae. Emu and cassowary faeces have abundant coarse unground material, including seeds, whereas deer and moa faeces are finely ground. The small pale objects in the moa coprolite are Coprosma seeds (c 2 mm length). Scale bars are 1 cm. Cassowary photo provided by Barbara Maslen; emu photo provided by Jason Smith.*

3.4.2 Seed size in coprolites versus gizzards

I analysed the sizes of 2253 seed remains identified from coprolites (Appendix 3.3) and 6786 seeds identified from gizzards (Fig. 3.4). The linear mixed effect model showed that seed length was significantly smaller in coprolites than in gizzards (LMM with a fixed effect for subfossil type and a random effect for sample nested within site: likelihood ratio test between full and null model: χ^2 (1) = 10.46, p = 0.0012). The weighted mean seed length in gizzards was 4.0 mm (± 0.02 S.E). The weighted mean seed size dispersed by moa (i.e. intact seeds in coprolites) was 1.64 mm (± 0.02 S.E), far smaller than the 4.6 mm (± 0.03 S.E) weighted mean seed size dispersed by New Zealand's smallest extant avian frugivore, the silvereye *Zosterops lateralis* (Fig. 3.5).

The largest-seeded species found in gizzards was from *E. hookerianus* (10.25 mm average length), while the largest found in coprolites was *Muehlenbeckia axillaris* (3.3 mm average length).

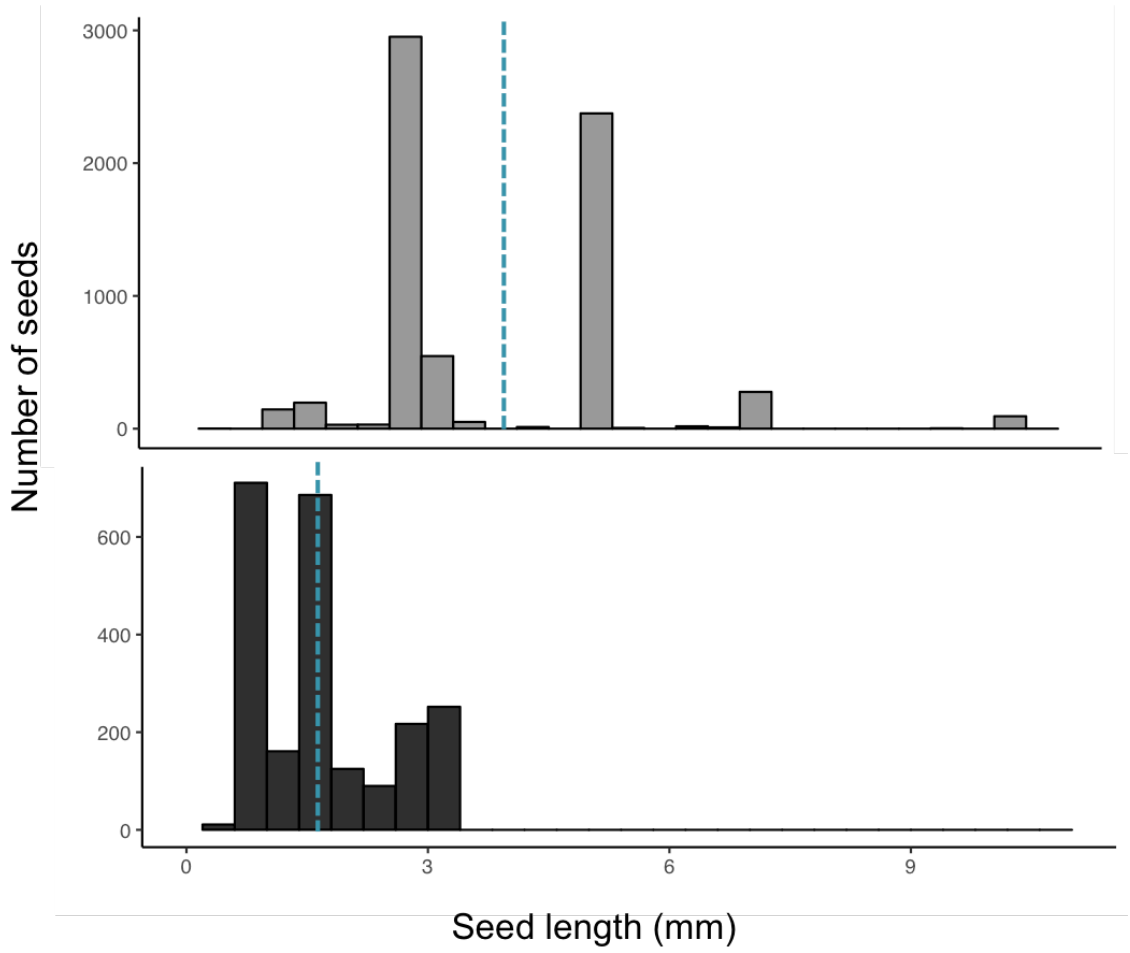


Figure 3.4. *Frequency distributions of seed length for seeds found in moa gizzards (light grey, upper) and moa coprolites (dark grey, lower). Means are marked by the dashed blue lines. Note the different y-axis scales.*

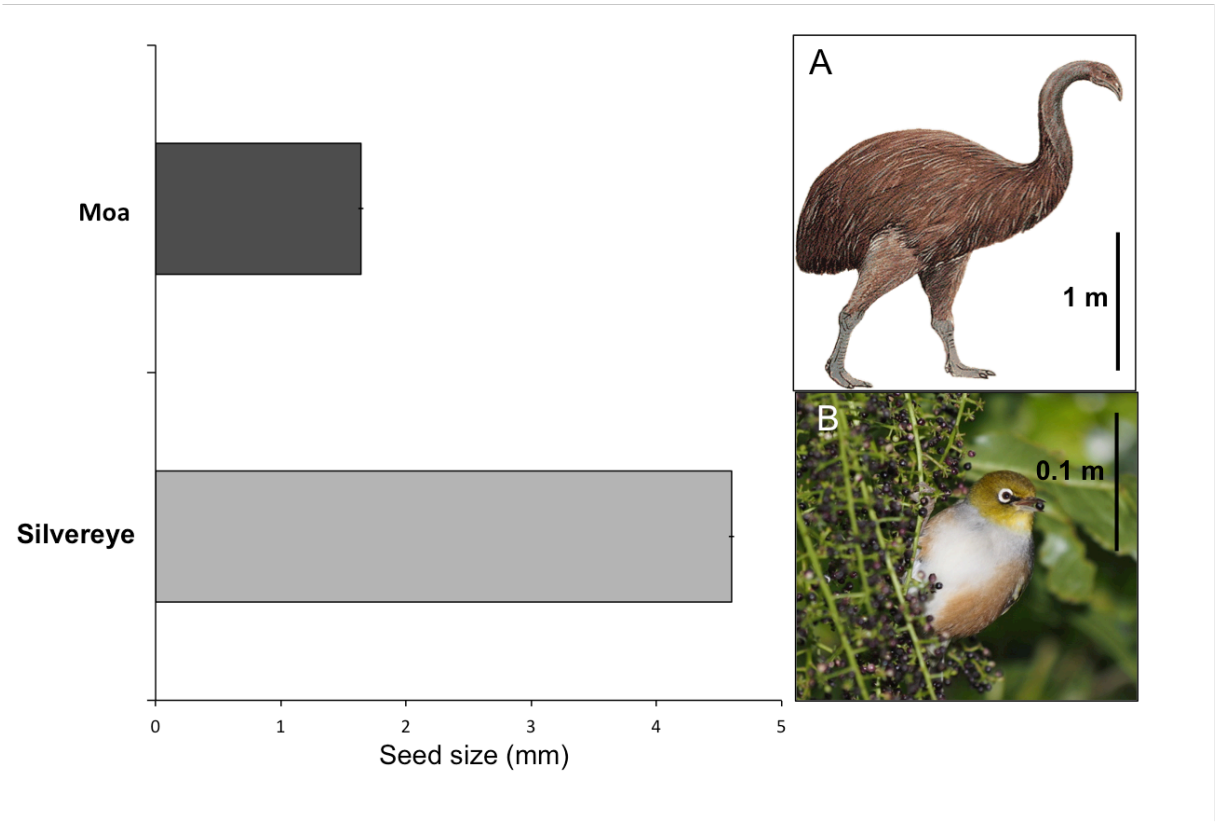


***Figure 3.5**. Mean seed size dispersed by (A) moa, weighing from 15 - 250 kilograms, and (B) silvereyes (Zosterops lateralis), weighing 0.01 – 0.013 kilograms. Error bars are standard error of the mean. Moa data for coprolites; silvereye data from (MacFarlane et al. 2015).*

3.4.3 Germination effects of simulated moa gut passage

Germination began 2.5 years after sowing for *Prumnopitys ferruginea* and was largely complete after 4 years, whereas for *Elaeocarpus dentatus* germination began after 1.6 years and continued for the remaining 5.6 years of observation. There was germination from untreated and mechanically-scarified seeds, but almost none from acid-scarified seeds for either *E. dentatus* or *P. ferruginea* (Appendix 3.4). Although mechanical scarification using stones in a concrete mixer (simulating moa gut passage) abraded and polished the endocarps, Cox Proportional Hazards models found that scarification did not decrease the time to germination for seeds that germinated within 7.2 years for either of the two species (χ^2 = 1.491, df = 5, p = 0.914 for *E.*

dentatus, Fig. 3.6; χ^2 = 3.1096, df = 2, p = 0.211 for *P. ferruginea*). For *E. dentatus,* seeds that were mechanically scarified had higher final total percentages germinating than whole or hand-cleaned seeds (hand-cleaned seeds simulate the effect of fruit pulp removal by an extant frugivore's gut) (χ^2 = 51.83, df = 2, p = <0.001). For *P. ferruginea,* there was no significant difference between the final percentages of germinated seeds for hand-cleaned and mechanically scarified treated seeds (χ^2 = 0.015, df = 1, p = 0.90). Overall, there was no evidence that the very slow germination of *E. dentatus* and *P. ferruginea* was an artifact of no longer passing through moa guts.

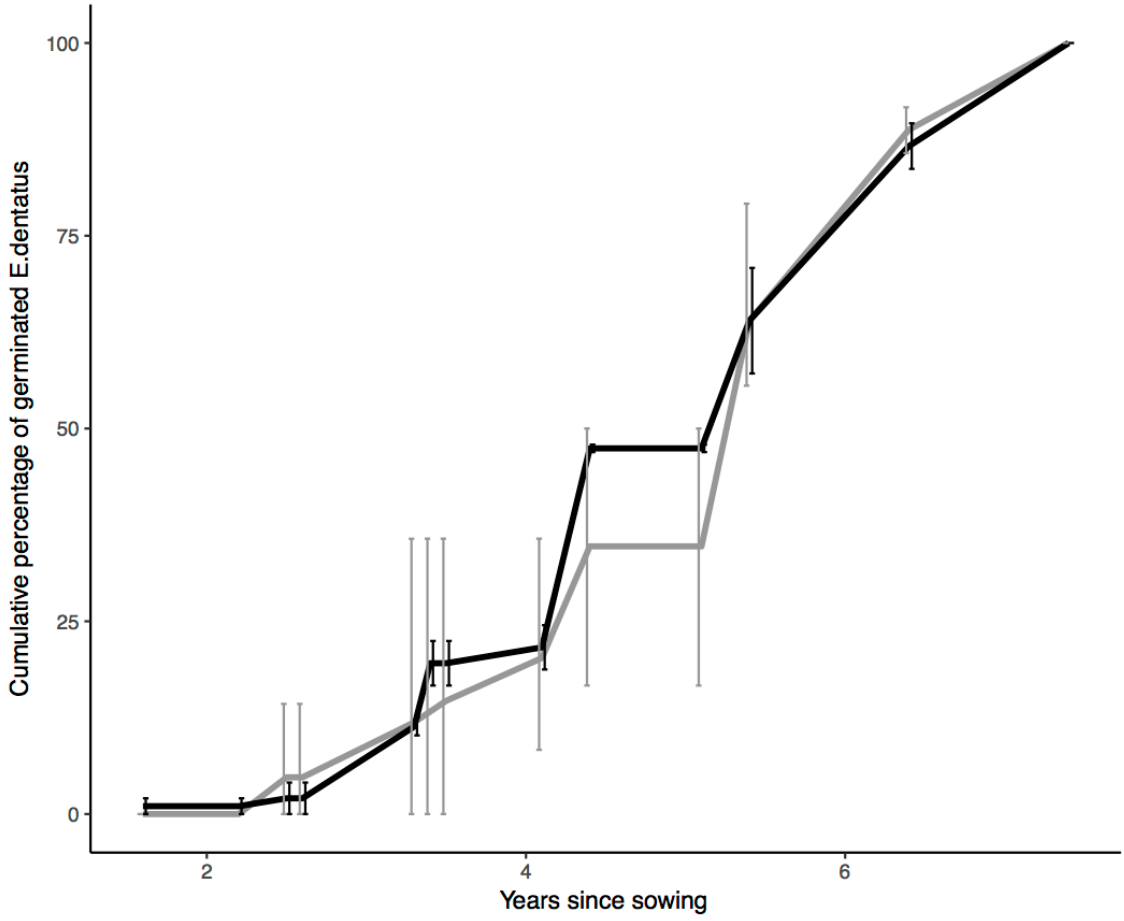


Figure 3.6. *Mean cumulative germination (%) against time for all E. dentatus seeds which germinated within 7.2 years, for mechanically scarified (black line) and non-scarified (grey line) treatments. Error bars are bootstrapped 95% confidence intervals.*

3.4.4 Endocarp strength tests

The mean force needed to rupture the endocarp of *Elaeocarpus dentatus* using a compression loaded MTS Criterion Model 43 was 927.4 (± 68.9 S.E) Newtons (N), with a maximum force of 1226.4 N.

3.5 Discussion

Understanding whether extinctions of large herbivores have created gaps in mutualistic networks is important when assessing the wider ecological consequences of their loss (Wood et al. 2017). Typically, large seeded plants (especially those with woody endocarps) are assumed to be most at risk of mutualistic disruption due to megafaunal extinctions (Janzen and Martin 1982; Guimarães et al. 2008; Galetti et al. 2017). However, my results show that while New Zealand's largest herbivore (the moa) consumed the large, thick-endocarp seeds of *Prumnopitys* and *Elaeocarpus* (as indicated by almost half of the gizzards containing them), they did not defecate these seeds intact. None of the 152 coprolites contained whole seeds larger than 3.3 mm, strongly suggesting that large seeds consumed by moa were ground by the gizzard into finely crushed particles. Small seeds generally pass through the gut of gizzard-containing birds faster than large seeds (Soons et al. 2008), and were probably subjected to less grinding and therefore higher survival rates than large seeds. Similarly, there is actually a significant negative relationship between animal body mass and ingested seed size across all vertebrates, mainly driven by the tendency for large ungulates to ingest small, dry seeds (Chen and Moles 2015). Birds, however, generally show a positive relationship between animal body mass and ingested seed size (Chen and Moles 2015), which further demonstrates how unusual moa are compared to their extant ratite relatives. Chen and Moles (2015) suggested that while interactions between large vertebrates and small seeds are often overlooked, they are actually very frequent, and this appears to hold true for moa. Wood et al. (2008) proposed that some of the small, dry seeds found in moa coprolites (e.g. *Einadia,* Poaceae) fit the "foliage is the fruit" dispersal syndrome, where dry indehiscent fruits closely associated with nutritious foliage are adapted for dispersal by large herbivores

(Janzen 1984). Paradoxically, the loss of moa's interactions with these seeds may be far more concerning than those interactions involving large seeds, as New Zealand has no other large native herbivores and the role of exotic deer and ungulates as seed dispersers is poorly documented.

3.5.1 Moa gizzards have no extant analogues

My results demonstrate that the grinding efficiency of the moa gizzard has no analogue in extant ratites, and possibly not in any extant bird. Moa gizzards were filled with up to 5.6 kg of stones (Burrows 1980) measuring up to 110 mm in length (Wood 2007). By comparison, emu (*Dromaius novaehollandiae*) gizzards contain up to 0.75 kg stones, with the largest stones only 47 mm in length (Webb 1994); ostriches (*Struthio* spp., the world's largest extant birds) carry 1 kg of gizzard stones (Wings and Sander 2007); and cassowaries' gizzards are poorly developed and hold few stones (Sales 2006). I found that *E. dentatus* endocarps required forces of 930 Newtons (equivalent to 95 kilograms of force) to rupture them and yet none survived moa gut passage, which further demonstrates the force moa gizzards must have exerted. This force is higher than those needed to rupture pecans (*Carya illinoinensis*), walnuts (*Juglans* spp.), and hazelnuts (*Corylus* spp.) (Schüler et al. 2014), but less than the forces needed to rupture endocarp-protected palm species consumed by ungulates in the Peruvian Amazon (Bodmer and Ward 2006). The intense grinding efficiency of the moa gizzard explains why the consistency of moa coprolites appears very fine, especially when visually compared to representative faecal deposits of other large extant ratites such as emus and cassowaries (Fig. 3). The reason why moa required such powerful grinding gizzards is unclear, although for the larger moa species it could be an adaptation to maximise digestion of their woody, low-nutrient diets (Wood et al. 2013b).

The more time that food spends in the gizzard, the longer it is subjected to grinding. The time that food takes to pass through the entire gut (including the gizzard) scales allometrically with herbivore body mass (Robbins 1993), and is influenced by diet (Afik and Karasov 1995), suggesting that moa gut passage times were probably very long. For example, 40 kg emus have been recorded taking an average of one to two days to

pass experimental pseudoseeds, with a number of pseudoseeds taking weeks and rarely even months to pass (Willson 1989). Fibrous foodstuffs likely increase gut passage time, so the wood and twig diet of certain moa species (Wood 2007) would have increased gut passage times further. For example, the diet of South Island giant moa (*D. robustus*) was largely beech twigs (Wood et al. 2013a): low-quality food which would have required considerable amounts of time in the gizzard to grind into small enough particles to pass through to the gut. These long passage times would have given the moa gastric mill more time to grind large seeds into small particles. However, it is possible that juvenile moa may have had less developed gizzards, which could not destroy large seeds. Similarly, if adult moa regurgitated seeds to their chicks the seeds may not have had adequate time in the adult bird's gizzard to be destroyed, although it is unlikely such seeds would be dispersed to suitable microsites. Given the large sample size of coprolites analysed in this study it is possible that some of the coprolites came from juvenile moa (especially as evidence suggests that some coprolites may be associated with nesting sites; Wood 2008), yet all of the coprolites had the same finely ground consistency with no intact large seeds.

Although these results convincingly demonstrate the destruction of large seeds by moa, it is worth noting that I only analysed fossil evidence from six of the nine species of moa, and that some subfossils could not be identified to species level. Therefore, there may be some differences between moa species that remain to be uncovered. However, all six moa genera were sampled so differences are likely to be small.

3.5.2 Anachronistic seeds: The "slaying of a beautiful hypothesis by an ugly fact"

While the seeds of *P. ferruginea, P. taxifolia, E. dentatus, E. hookerianus* and *V. lucens* appear ill-suited for dispersal by the contemporary fauna, I have shown that they almost certainly did not survive passage through the stone-filled gizzards of moa, and therefore are not anachronistic seeds adapted for dispersal by these giant ratites. Germination of most of these plant species is slow to extremely slow (Kelly et al. 2010), and in fact I know of no other large-seeded tree where germination of unburied seeds continues for more than 7 years as in *E. dentatus*. While small, rounded seeds

tend to get incorporated into the soil profile and if buried often delay germination for years (Moles et al. 2000), it is extremely unusual to have such slow germination in large-seeded tree species. While I aimed to test whether simulated moa gut passage increased germination speed in two of these species, this study has revealed that 4 hours in a concrete mixer would have been a poor proxy for the powerful grinding action of a moa gizzard. But even gentle seed coat abrasion in the concrete mixer failed to hasten germination for *P. ferruginea* or *E. dentatus,* so these species' extremely slow germination cannot be explained by the extinction of moa. It is possible that the long germination times of seeds from these long-lived tree species are advantageous as they facilitate dispersal in time as well as space (Kelly et al. 2004). Additionally, early germination is not beneficial under all circumstances, as demonstrated by early germinating individuals of *Linum catharticum* and *Gentianella amarella* doing worse than those that germinated later (Kelly 1989). Perhaps slow germination in canopy trees is favoured by New Zealand's high proportion of mast-seeding plants (Kelly and Sork 2002) and low pre-human rates of disturbance (Kelly and Sullivan 2010), meaning that trees had more need than in other parts of the world for delayed germination to exploit canopy gaps.

While I have demonstrated that the large size of these seeds is not an adaptation for moa dispersal, their size probably confers other advantages, such as increased seedling survival. Seedlings that emerge from large seeds have been shown to be more tolerant of the many hazards encountered during establishment (e.g. drought, defoliation, shading)(Moles and Westoby 2004). Large seeded tree species also typically have larger canopies and more reproductive years than small seeded species, which provides a reproductive benefit (Moles and Westoby 2004). It is also important to note that while these seeds are large by New Zealand standards, they are still within the gape size of New Zealand's largest extant frugivore, the kererū (*Hemiphaga novaeseelandiae*).

Despite the unsolved puzzle of slow germination times, the remaining dispersal syndrome (early abscission, low contemporary dispersal rates, and visibility on the forest floor) of *Elaeocarpus* fruits suggest that they may be adapted for dispersal by flightless birds with less destructive gizzards (Lord 2002; Carpenter et al. 2017). For

example, in Australia *Elaeocarpus* species are dispersed by cassowaries (Bradford and Westcott 2010). Flightless birds made up a significant proportion of the New Zealand avifauna (Atkinson and Millener 1991), and the seed dispersal services these taxa provide are still largely unknown. Both North Island brown kiwi (*Apteryx mantelli,* an endemic ratite) and weka (*Gallirallus australis,* an endemic flightless rail) have been recorded consuming *Elaeocarpus* fruits (Clout and Hay 1989). I found that the final germination percentage of *E. dentatus* seeds increased with mechanical scarification, so it could be that the grit in kiwi and weka gizzards also abrades the seedcoat enough to increase the number of seeds that germinate. Additionally, volant frugivores such as the kererū have been recorded consuming *Elaeocarpus dentatus* fruits from the forest floor (see Chapter 4).

3.5.3 Conclusions

This study overturns widely held suppositions about moa as important dispersers of large seeds in pre-human New Zealand, and therefore contradicts assumptions that extinct herbivorous megafauna dispersed the largest seeds. While moa consumed seeds up to ~10 mm length, which are the largest seeds occurring in the areas yielding subfossil samples, the only seeds that survived their formidable grinding gizzards were less than 3.3 mm long. Therefore, New Zealand's largest herbivores only dispersed small seeds, such as those of dryland 'spring annual' herbs (Wood et al. 2008). The loss of moa interactions with these small-seeded plants (some of which are now endangered; Rogers et al. 2002) may paradoxically represent the actual gap in contemporary seed dispersal services. However, overall my results show that moa would have left little in the way of a seed dispersal gap, and focus should fall back to how New Zealand dispersal is faring with reduced populations and range sizes of extant seed dispersers (Kelly et al. 2010).

These findings highlight the importance of using multiple lines of evidence when investigating the ecosystem roles of extinct fauna rather than simply relying on plausible assumptions. While the discovery of subfossil gizzard contents revealed important information on moa diet, it is only the subsequent recent discovery and analysis of large numbers of coprolites that have revealed that moa did not in fact

disperse large or even medium-sized seeds. Similarly, although using the “ghosts of past mutualisms” to explain the existence of strange, apparently maladapted flora is appealing, further lines of evidence are required before gaps can be confirmed to be present in contemporary seed dispersal networks. This study also demonstrates the value of long-term palaeoecological data to help inform ecology and identify biological vulnerability and resilience (Dietl et al. 2015). With contemporary ecosystems undergoing significant environmental change, studies that use palaeoecological data to determine ecological baselines are becoming increasingly relevant (Wilmshurst et al. 2014; Dietl et al. 2015). While the majority of these studies have examined how taxa respond to environmental change, here I showcase how palaeoecological data (in particular, coprolite analysis) can also yield precious information on lost interaction networks (see also Boast et al. 2018).

3.6 Appendices

3.6.1 Description of putative moa-adapted fruits

All five species have drupaceous fruits that ripen and fall in the New Zealand autumn (February – May). *Elaeocarpus dentatus* fruits are fleshy, purple-black in colour, and measure an average of 9.4 mm in diameter. They have a high percentage of flesh (about 25%) with a high dry matter content (approximately 44%). The thick endocarp is deeply furrowed and wrinkled. *Elaeocarpus hookerianus* fruits are brown or dark purple (mean diameter 7.2 mm) and more elongate than *E. dentatus* fruits.

The two *Prumnopitys* species are gymnosperms, and therefore they technically produce single-seeded cones, but will be referred to as fruits here as these cones ecologically function as fruits. *Prumnopitys ferruginea* produces reddish-pink fruits from 12 to 15 mm in diameter consisting of a fleshy exocarp surrounding a large seed with a woody endocarp (1.5-2 mm thick), encasing the endosperm. The fruit is fleshy, oily, and smells and tastes strongly of terpenes. *Prumnopitys taxifolia* produces fleshy, oily, aromatic, terpene-tasting, purple- black drupes with a glaucous bloom (mean diameter 9.4 mm).

Vitex lucens fruit is a red, bright pink, or white drupe (15 mm mean fruit diameter) containing a woody endocarp that encloses four cells, each of which may produce one seed.

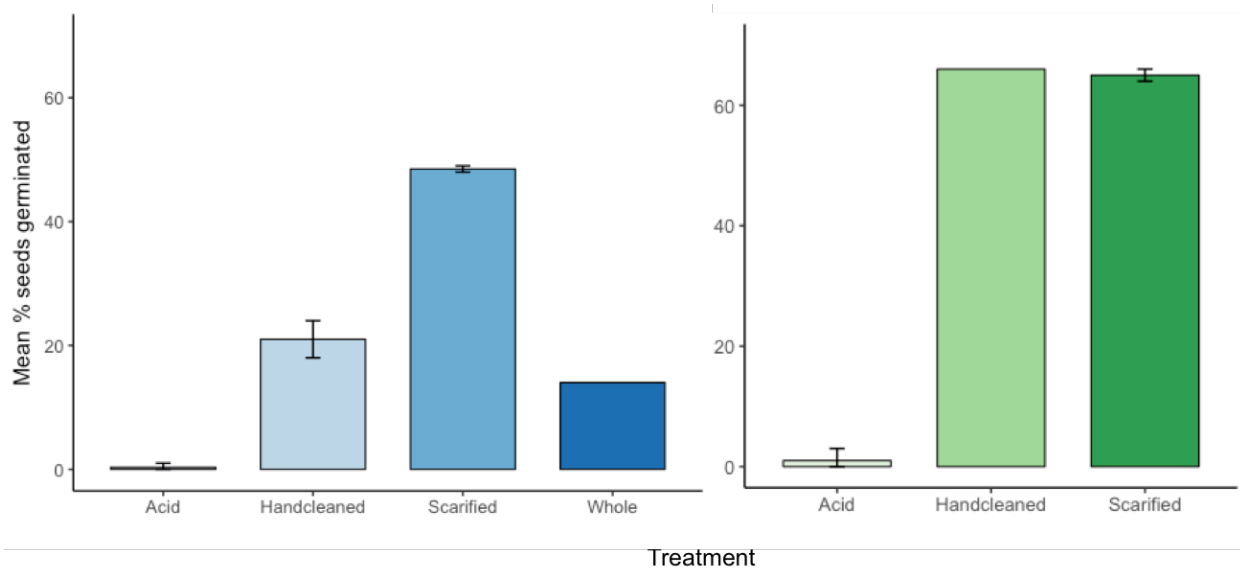
3.6.2 Evidence for presence of *Prumnopitys* and *Elaeocarpus* at sites where gizzards or coprolites were recovered from

Site	Evidence	Number of coprolites analysed	Number of gizzards analysed
Euphrates Cave	*Elaeocarpus* aDNA and *Prumnopitys* pollen in coprolites	35	0
Dart River	Oxidales aDNA and *Prumnopitys* pollen in coprolites	89	0
Mt. Nicholas	*Prumnopitys* seeds in surrounding soil layer. *Prumnopitys* pollen in coprolites.	2	0
Cheviot/Pyramid Valley	*Elaeocarpus* and *Prumnopitys* seeds present in gizzards	0	18
Scaifes' Lagoon	*Elaeocarpus* and *Prumnopitys* seeds present in gizzards	0	4

3.6.3 Plant species and size of seeds that have been identified from coprolites

Species	Sum of seeds in coprolites	Mean seed length (mm)	Comments
Acaena	1	NA	
Asteraceae	33	NA	
Carex	41	1.7	
Carmichaelia	1	NA	
Ceratocephala_pungens	16	1.5	
Colobanthus	11	0.6	
Coprosma	172	2.98	
Coprosma_petriei	82	2.4	
Coriaria	87	2	
Coriaria_plumosa	14	1.95	
Cyperaceae	21	NA	
Einadia_allani	52	1.25	
Einadia_triandra	21	1.55	
Fuchsia_excorticata	26	0.8	
Gaultheria_or_Pernettya	561	0.62	
Gonocarpus	16	2.15	
Gymnosperm	3	NA	Not intact
Juncus	43	2.845	
Lagenifera_pumila	8	2.2	
Leucopogon_fraseri	214	3.25	
Lobeliaceae_cf_Pratia	103	0.75	
Melicytus	2	3.025	
Muehlenbeckia_axillaris	36	3.3	
Myosotis_pygmaea	1	1.35	
Myosurus_minimus	18	1.35	
Oxalis_exilis	22	1.1	
Poaceae	7	NA	
Podocarp	1	NA	Not intact
Pratia_angulata	9	0.75	
Ranunculus	89	1.6	
Ranunculus_gracilipes	464	1.6	
Rubus	2	2.7	
Scirpus	55	1.5	
Urtica	68	1.24	
Veronica (Hebe)	8	2.47	
Wahlenbergia	12	0.7	

3.6.4 Germination results



Appendix 3.6.4. Final germination percentages of Elaeocarpus dentatus (blue, left) and Prumnopitys ferruginea (green, right) seeds treated with acid, mechanical scarification, handcleaning, and left whole (untreated). Error bars are bootstrapped standard error of the mean.

3.7 References

Afik D, Karasov WH (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. Ecology 76:2247–2257 . doi: 10.2307/1941699

Atkinson IAE, Millener PR (1991) An ornithological glimpse into New Zealand's pre-human past. Proc 20th Int Ornithol Congr 1:129–192

Baños-Villalba A, Blanco G, Díaz-Luque JA, et al (2017) Seed dispersal by macaws shapes the landscape of an Amazonian ecosystem. Sci Rep 7:1–12 . doi: 10.1038/s41598-017-07697-5

Barlow C (2002) Anachronistic fruits and the ghosts who haunt them. Arnoldia 61:14–21

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1–48 . doi: 10.18637/jss.v067.i01

Boast AP, Weyrich LS, Wood JR, et al (2018) Coprolites reveal ecological interactions lost with the extinction of New Zealand birds. Proc Natl Acad Sci 115:1546–1551 . doi: 10.1073/pnas.1712337115

Bodmer R, Ward D (2006) Frugivory in large mammalian herbivores. Large Herbiv Ecol Ecosyst Dyn Conserv 232–260 . doi: 10.1017/CBO9780511617461.010

Bradford MG, Westcott DA (2010) Consequences of southern cassowary (Casuarius casuarius, L.) gut passage and deposition pattern on the germination of rainforest seeds. Austral Ecol 35:325–333 . doi: 10.1111/j.1442-9993.2009.02041.x

Bunce M, Worthy TH, Phillips MJ, et al (2009) The evolutionary history of the extinct ratite moa and New Zealand Neogene paleogeography. Proc Natl Acad Sci 106:20646–20651 . doi: 10.1073/pnas.0906660106

Burns KC (2013) What causes size coupling in fruit-frugivore interaction webs? Ecology 94:295–300 . doi: 10.1890/12-1161.1

Burrows CJ (1980) Some empirical information regarding the diet of moas. N Z J Ecol 125–130

Carpenter JK, Kelly D, Clout MN, et al (2017) Trends in the detections of a large frugivore (Hemiphaga novaeseelandiae) and fleshy-fruited seed dispersal over three decades. N Z J Ecol 41:41–46 . doi: 10.20417/nzjecol.41.17

Chen SC, Moles AT (2015) A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. Glob Ecol Biogeogr 24:1269–1280 . doi: 10.1111/geb.12346

Clout MN, Hay JR (1989) The importance of birds As browsers, pollinators and seed

dispersers in New Zealand forests. N Z J Ecol 27–33 . doi: 10.2307/24053245

Dietl GP, Kidwell SM, Brenner M, et al (2015) Conservation paleobiology: Leveraging knowledge of the past to inform conservation and restoration. Annu Rev Earth Planet Sci 43:79–103 . doi: 10.1146/annurev-earth-040610-133349

Falla RA (1941) Preliminary report on excavations at Pyramid Valley, Waikari, North Canterbury. Rec Canterbury Museum 4:325–326

Federman S, Dornburg A, Daly DC, et al (2016) Implications of lemuriform extinctions for the Malagasy flora. Proc Natl Acad Sci 113:5041–5046 . doi: 10.1073/pnas.1523825113

Figuerola J, Charalambidou I, Santamaria L, Green AJ (2010) Internal dispersal of seeds by waterfowl: Effect of seed size on gut passage time and germination patterns. Naturwissenschaften 97:555–565 . doi: 10.1007/s00114-010-0671-1

Fritz J, Hummel J, Kienzle E, et al (2011) Gizzard vs. teeth, it's a tie: food-processing efficiency in herbivorous birds and mammals and implications for dinosaur feeding strategies. Paleobiology 37:577–586 . doi: 10.1666/10031.1

Galetti M, Mole M, Jordano P, et al (2017) Ecological and evolutionary legacy of megafauna extinctions. Biol Rev. doi: 10.1111/brv.12374

Gillespie R, Camens AB, Worthy TH, et al (2012) Man and megafauna in Tasmania: Closing the gap. Quat Sci Rev 37:38–47 . doi: 10.1016/j.quascirev.2012.01.013

Griffiths CJ, Hansen DM, Jones CG, et al (2011) Resurrecting extinct interactions with extant substitutes. Curr Biol 21:762–765 . doi: 10.1016/j.cub.2011.03.042

Guimarães PR, Galetti M, Jordano P (2008) Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. PLoS One 3:e1745 . doi: 10.1371/journal.pone.0001745

Horrocks M, D'Costa D, Wallace R, et al (2004) Plant remains in coprolites: Diet of a subalpine moa (Dinornithiformes) from southern New Zealand. Emu 104:149–156 . doi: 10.1071/MU03019

Huynen L, Gill BJ, Millar CD, Lambert DM (2010) Ancient DNA reveals extreme egg morphology and nesting behavior in New Zealand's extinct moa. Proc Natl Acad Sci 107:16201–16206 . doi: 10.1073/pnas.0914096107

Janzen DH (1984) Dispersal of small seeds by big herbivores: Foliage is the fruit. Am Nat 123:338 . doi: 10.1086/284208

Janzen DH, Martin PS (1982) Neotropical anachronisms : The fruits the Gomphotheres ate. Science (80-) 215:19–27

Johnson C. (2009) Ecological consequences of Late Quaternary extinctions of megafauna. Proc R Soc B Biol Sci 276:2509–2519 . doi: 10.1098/rspb.2008.1921

Kelly D (1989) Demography of short-lived plants in chalk grassland. Life cycle variation in annuals and strict biennials. J Ecol 77:747–769 . doi: 10.2307/2260983

Kelly D, Ladley JJ, Robertson AW, et al (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit- dispersal in New Zealand. N Z J Ecol 34:66–85

Kelly D, Ladley JJ, Robertson AW (2004) Is dispersal easier than pollination? Two tests in New Zealand Loranthaceae. New Zeal J Bot 42:89–103

Kelly D, Sork VL (2002) Mast seeding in perennial plants: Why, how, where? Annu Rev Ecol Syst 33:427–447 . doi: 10.1146/annurev.ecolsys.33.020602.095433

Kelly D, Sullivan J. (2010) Life histories, dispersal, invasions, and global change - progress and prospects in New Zealand ecology, 1989–2029. N Z J Ecol 34:86–114

Koch PL, Barnosky AD (2006) Late Quaternary extinctions: State of the debate. Annu Rev Ecol Evol Syst 37:215–250 . doi: 10.1146/annurev.ecolsys.34.011802.132415

Lee WG, Clout MN, Robertson HA, Bastow Wilson J (1991) Avian dispersers and fleshy fruits in New Zealand. Proc Int Orn Congr XX 1617–1623

Lee WG, Wood JR, Rogers GM (2010) The ecological transformation of Aotearoa/New Zealand Legacy of avian-dominated plant–herbivore systems in New Zealand. N Z J Ecol 34:28–47

Lord J (2002) Have frugivores influenced the evolution of fruit traits in New Zealand? In: DJ L, WR S, M G (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, WallingfoRd, UK, pp 55–68

MacFarlane AET, Kelly D, Briskie J V (2015) Introduced blackbirds and song thrushes: Useful substitutes for lost mid-sized native frugivores, or weed vectors? N Z J Ecol 40: . doi: 10.20417/nzjecol.40.9

Mcdowell MC, Prideaux GJ, Walshe K, et al (2015) Re-evaluating the Late Quaternary fossil mammal assemblage of Seton Rockshelter, Kangaroo Island, South Australia, including the evidence for late-surviving megafauna. J Quat Sci 30:355–364 . doi: 10.1002/jqs.2789

McNair JN, Sunkara A, Frobish D (2012) How to analyse seed germination data using statistical time-to-event analysis: non-parametric and semi-parametric methods. Seed Sci Res 22:77–95 . doi: 10.1017/S0960258511000547

Midgley JJ, Illing N (2009) Were Malagasy Uncarina fruits dispersed by the extinct elephant bird? S Afr J Sci 105:467–469

Moles AT, Hodson DW, Webb CJ (2000) Seed size and shape and persistence in the soil in the New Zealand flora. Oikos 89:541–545 . doi: 10.1034/j.1600-0706.2000.890313.x

Moles AT, Westoby M (2004) Seedling survival and seed size: A synthesis of the literature. J Ecol 92:372–383 . doi: 10.1111/j.0022-0477.2004.00884.x

Moore L, Edgar B (1970) Flora of New Zealand, Vol. II. Government Printer, Wellington, New Zealand

Murray P, Vickers-Rich P (2004) Magnificent Mihirungs. The Colossal Flightless Birds of the Australian Dreamtime. Indiana University Press

Otto R, Garzón-Machado V, del Arco M, et al (2017) Unpaid extinction debts for endemic plants and invertebrates as a legacy of habitat loss on oceanic islands. Divers Distrib 23:1031–1041 . doi: 10.1111/ddi.12590

Perry GLW, Wheeler AB, Wood JR, Wilmshurst JM (2014) A high-precision chronology for the rapid extinction of New Zealand moa (Aves, Dinornithiformes). Quat Sci Rev 105:126–135 . doi: 10.1016/j.quascirev.2014.09.025

Pires MM, Guimarães PR, Galetti M, Jordano P (2018) Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. Ecography (Cop) 41:153–163 . doi: 10.1111/ecog.03163

Rawlence N, Wood J, Scofield R, et al (2013) Soft-tissue specimens from pre-European extinct birds of New Zealand. J. R. Soc. New Zeal. 43:154–181

Robbins C (1993) Wildlife feeding and nutrition. Academic Press, New York

Robertson AW, Trass A, Ladley JJ, Kelly D (2006) Assessing the benefits of frugivory for seed germination: The importance of the deinhibition effect. Funct. Ecol. 20:58–66

Rogers G, Walker S, Tubbs M, Henderson J (2002) Ecology and conservation status of three “spring annual” herbs in dryland ecosystems of New Zealand. New Zeal J Bot 40:649–669 . doi: 10.1080/0028825X.2002.9512821

Sales J (2006) Digestive physiology and nutrition of ratites. Avian Poult Biol Rev 17:41–55 . doi: 10.3184/147020606783437912

Schüler P, Speck T, Bührig-Polaczek A, Fleck C (2014) Structure-function relationships in Macadamia integrifolia seed coats - Fundamentals of the hierarchical microstructure. PLoS One 9:e102913 . doi: 10.1371/journal.pone.0102913

Soons MB, Van Der Vlugt C, Van Lith B, et al (2008) Small seed size increases the potential

for dispersal of wetland plants by ducks. J Ecol 96:619–627 . doi: 10.1111/j.1365-2745.2008.01372.x

Stocker GC, Irvine AK (1983) Seed dispersal by cassowaries (Casuarius casuarius) in North Queensland's rainforests. Biotropica 15:170–176 . doi: 10.2307/2387825

Thorsen MJ, Seddon PJ, Dickinson KJM (2011) Faunal influences on New Zealand seed dispersal characteristics. Evol Ecol 25:1397–1426 . doi: 10.1007/s10682-011-9470-1

Webb C (1994) Lithic assemblage formation in semi-arid Australia: the role of Emu gastroliths. J. Archaeol. Sci. 21(2):145–152

Webb CJ, Simpson MJA (2001) Seeds of New Zealand Gymnosperms and Dicotyledons. Manuka Press

Westcott DA, Bentrupperbäumer J, Bradford MG, McKeown A (2005) Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. Oecologia 146:57–67 . doi: 10.1007/s00442-005-0178-1

Willson MF (1989) Gut retention times of experimental pseudoseeds by Emus. Biotropica 21:210–213 . doi: 10.2307/2388645

Wilmshurst JM, Moar NT, Wood JR, et al (2014) Use of pollen and ancient DNA as conservation baselines for offshore islands in New Zealand. Conserv Biol 28:202–212 . doi: 10.1111/cobi.12150

Wings O, Sander PM (2007) No gastric mill in sauropod dinosaurs: new evidence from analysis of gastrolith mass and function in ostriches. Proc R Soc B Biol Sci 274:635–640 . doi: 10.1098/rspb.2006.3763

Wood JR (2007) Moa gizzard content analyses: further information on the diet of Dinornis robustus and Emeus crassus, and the first evidence for the diet of Pachyornis elephantopus (Aves: Dinornithiformes). Rec Canterbury Museum 21:27–39

Wood JR (2008) Moa (Aves: Dinornithiformes) nesting material from rockshelters in the semi-arid interior of South Island, New Zealand. J R Soc New Zeal 38:115–129 . doi: 10.1080/03014220809510550

Wood JR, Perry GLW, Wilmshurst JM (2017) Using palaeoecology to determine baseline ecological requirements and interaction networks for de-extinction candidate species. Funct. Ecol. 31:1012–1020

Wood JR, Rawlence NJ, Rogers GM, et al (2008) Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes). Quat Sci Rev 27:2593–2602 . doi: 10.1016/j.quascirev.2008.09.019

Wood JR, Wilmshurst JM (2017) Changes in New Zealand forest plant communities following the prehistoric extinction of avian megaherbivores. J Veg Sci 28:160–171 . doi: 10.1111/jvs.12469

Wood JR, Wilmshurst JM (2014) Late Quaternary terrestrial vertebrate coprolites from New Zealand. Quat Sci Rev 98:33–44 . doi: 10.1016/j.quascirev.2014.05.020

Wood JR, Wilmshurst JM, Richardson SJ, et al (2013a) Resolving lost herbivore community structure using coprolites of four sympatric moa species (Aves: Dinornithiformes). Proc Natl Acad Sci USA 110:16910–16915 . doi: 10.2307/23750685?ref=search-gateway:44c92500ffa3ab05bb979b5d8bdfd7b5

Wood JR, Wilmshurst JM, Wagstaff SJ, et al (2012a) High-resolution coproecology: Using coprolites to reconstruct the habits and habitats of New Zealand's extinct upland Moa (Megalapteryx didinus). PLoS One 7:e40025 . doi: 10.1371/journal.pone.0040025

Wood JR, Wilmshurst JM, Worthy TH, Cooper A (2012b) First coprolite evidence for the diet of Anomalopteryx didiformis, an extinct forest ratite from New Zealand. N Z J Ecol 36:164–170

Worthy TH, Holdaway RN (2002) The Lost World of the Moa. Canterbury University Press, Christchurch, New Zealand

UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

Deputy Vice-Chancellor's Office
Postgraduate Research Office

Co-Authorship Form

This form is to accompany the submission of any thesis that contains research reported in co-authored work that has been published, accepted for publication, or submitted for publication. A copy of this form should be included for each co-authored work that is included in the thesis. Completed forms should be included at the front (after the thesis abstract) of each copy of the thesis submitted for examination and library deposit.

Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter 4, published in Ecology and Evolution

Carpenter JK, Kelly D, Moltchanova E, O'Donnell CFJ. 2018. "Introduction of mammalian seed predators and the loss of an endemic flightless bird impair seed dispersal of the New Zealand tree Elaeocarpus dentatus". Ecology and Evolution.

Please detail the nature and extent (%) of contribution by the candidate:

Jo Carpenter formulated research questions, designed the study, conducted fieldwork, analysed the data (with the exception of the Bayesian analysis), created graphs, and wrote the manuscript (80%).

Certification by Co-authors:

If there is more than one co-author then a single co-author can sign on behalf of all

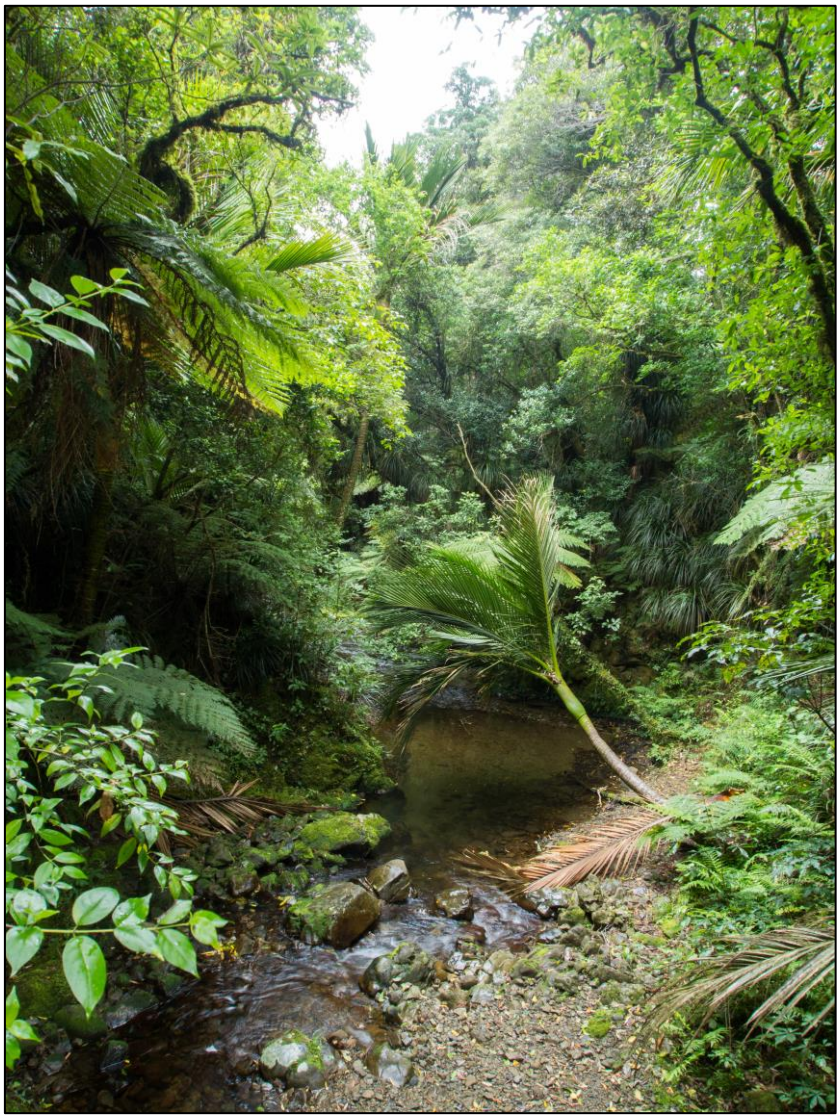
The undersigned certifies that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name: Dave Kelly Signature: Dave Kelly Date: *6/2/2019*

4

Introduction of mammalian seed predators and the loss of an endemic flightless bird impair seed dispersal of the New Zealand tree *Elaeocarpus dentatus*



Catchpool Valley, Wellington: A mainland site where hīnau were monitored

4.1 Abstract

Understanding the mutualistic services provided by species is critical when considering both the consequences of their loss or the benefits of their reintroduction. Like many other Pacific islands, New Zealand seed dispersal networks have been changed by both significant losses of large frugivorous birds and the introduction of invasive mammals. These changes are particularly concerning when important dispersers remain unidentified. I tested the impact of frugivore declines and invasive seed predators on seed dispersal for an endemic tree, hīnau *Elaeocarpus dentatus,* by comparing seed dispersal and predation rates on the mainland of New Zealand with offshore sanctuary islands with higher bird and lower mammal numbers. I used cameras and seed traps to measure predation and dispersal from the ground and canopy, respectively. I found that canopy fruit handling rates (an index of dispersal quantity) were poor even on island sanctuaries (only 14% of seeds captured below parent trees on islands had passed through a bird), which suggests that hīnau may be adapted for ground-based dispersal by flightless birds. Ground-based dispersal of hīnau was low on the New Zealand mainland compared to sanctuary islands (4% of seeds dispersed on the mainland vs.76% dispersed on islands), due to low frugivore numbers. A flightless endemic rail (*Gallirallus australis*) conducted the majority of ground-based fruit removal on islands. Despite being threatened, this rail is controversial in restoration projects because of its predatory impacts on native fauna. Our study demonstrates the importance of testing which species perform important mutualistic services, rather than simply relying on logical assumptions.

4.2 Introduction

Drivers of global environmental change such as habitat loss, illegal harvesting, and biological invasions have had negative impacts on frugivorous, seed dispersing species, sparking concern for the functioning of seed dispersal networks (Sekercioglu et al. 2004). Frugivorous animals influence the survival, community dynamics (Wright et al. 2000), and spatial and genetic patterns of plants (Nathan and Muller-Landau 2000; Levine and Murrell 2003), so frugivore declines can have significant cascading effects, although these consequences are frequently masked by the long life span of perennial plants (McConkey et al. 2012). Many ecosystems are already suffering from low biodiversity following hundreds of years of human impacts, which further exacerbates the effects of recent disperser declines (Corlett 2007; O'Farrill et al. 2013). Although some cascading effects such as impaired plant recruitment have been documented (e.g. Christian 2001, Wotton & Kelly 2011, Rogers *et al.* 2017), the effects of frugivore losses on their mutualistic partners are complex and still poorly understood. This is particularly true when unexpected animals are acting as seed dispersers (Calviño-Cancela 2002; Young et al. 2012); or where unusual dispersal mechanisms occur that may have been overlooked (e.g. Wallace et al. 2008).

In addition to declines in frugivores, ecosystems worldwide have suffered from biological invasions. Invading species have the potential to either directly alter seed dispersal networks, by the establishment of novel interactions with native biota, or indirectly alter seed dispersal networks, by affecting the abundance, behaviour, or distribution of native biota (McConkey et al. 2012). Invasive mammals such as rodents are particularly pervasive and problematic, with ship rats (*Rattus rattus*) having invaded over 80% of the world's island groups (Towns 2009). Rodents have the capacity to damage seed dispersal interactions by destroying or depredating (I will use these two terms synonymously) seeds (Pender et al. 2013; Shiels and Drake 2015) and preying upon native frugivores (Towns et al. 2006). While the impacts of exotic mammals on populations of frugivores have been well established (Doherty et al. 2016), the synergistic effects of exotic mammalian seed predators and declines in

native dispersers are largely unknown (McConkey et al. 2012, but see Wotton and Kelly 2011), despite their ubiquity.

New Zealand unfortunately offers an ideal opportunity to test the effects of frugivore declines and exotic mammals on seed dispersal services. The archipelago's 80 million year isolation from other landmasses has created an unusual suite of frugivores, dominated by birds and lizards and almost entirely devoid of mammals (Kelly et al. 2010; Wotton et al. 2016). Since the arrival of humans in ca. 1280 (Wilmshurst et al. 2008) almost half (41%) of New Zealand's endemic avifauna has gone extinct, including many frugivores (Innes et al. 2010). These considerable losses are partly due to the introduction of mammalian predators, including three species of rat (Polynesian rat *Rattus exulans*, Norway rat *Rattus norvegicus* and ship rat *Rattus rattus*), mice *Mus musculus*, cats *Felis catus*, mustelids (Mustelidae), and brushtail possums *Trichosurus vulpecula* (Towns et al. 2006). These mammals affect seed dispersal both indirectly, by preying upon frugivore populations (e.g. Clout *et al.* 1995, Starling-Windhof *et al.* 2011, Innes *et al.* 2010), and directly through seed, fruit, and flower predation (Beveridge 1964; Campbell and Atkinson 2002). For example, Wotton and Kelly (2011) demonstrated that the synergistic effects of frugivore loss and mammalian seed predation reduced recruitment of two large-seeded New Zealand trees by >92%.

So far, investigations into the functioning of New Zealand's seed dispersal networks have focused on volant frugivorous birds (Kelly et al. 2010). However, flightless frugivores were a substantial part of New Zealand's historic avifauna, and the role that these species play in seed dispersal is still unclear. Understanding whether flightless birds are significant seed dispersers in New Zealand may also provide information on whether removal of fruits by ground based birds is an important mechanism on other oceanic islands where flightlessness is common (e.g. Polynesia). Like Polynesia (Olson and James 1991; Steadman 1995), a large proportion of the birds in this guild have gone extinct in New Zealand (66%: Atkinson and Millener 1991; Tennyson 2009). One species that remains is the endemic weka (*Gallirallus australis*), a charismatic flightless rail that has become severely range restricted due to mammalian predation and possible climate-related starvation (Beauchamp et al. 1999). Their large gape and frequent consumption of fruit suggests they may be significant seed dispersers (Carroll

1963; Coleman et al. 1983), but their predatory impacts on other native fauna have lead to them becoming regarded negatively by conservationists (Miskelly and Beauchamp 2004). Their predatory behaviour has resulted in the removal of weka from at least eleven islands where humans had introduced them (Miskelly and Beauchamp 2004), and even from some islands where they occurred naturally (e.g. Anchor Island, Fiordland).

Ground collection of fruit by flightless birds such as weka is likely to have been an important dispersal mechanism for many plant species, particularly those with larger fruits (Lee et al. 1991; Thorsen et al. 2011). For example, in Australia cassowaries (*Casuarius* spp.) and emus (*Dromaius novaehollandiae*) remove a significant proportion of seeds from the ground (Calviño-Cancela et al. 2006; Bradford and Westcott 2010). Lord (2002) speculated that seeds that were adapted for dispersal by flightless birds should fall to the ground when ripe and be conspicuous on the forest floor. One species that meets these criteria is hīnau (*Elaeocarpus dentatus*: Elaeocarpaceae), an endemic forest tree with large, shiny dark brown fruits that feature a very thick endocarp and drop to the ground when ripe (Lord 2002). Hīnau currently appears to have very low seed dispersal rates from the canopy (Carpenter et al. 2017) but it is unclear whether these low rates are due to low local numbers of volant frugivores, or because its seeds are adapted for ground removal by flightless frugivores. The only extant frugivores recorded consuming hīnau fruits are volant kererū (*Hemiphaga novaeseelandiae*) and kōkako (*Callaeas wilsoni*), and flightless weka and brown kiwi (*Apteryx mantelli*) (Clout and Hay 1989; Kelly et al. 2010), three of which (kōkako, brown kiwi, and weka) are severely range restricted. Additionally, rats and feral pigs (*Sus scrofa*) have been recorded destroying hīnau seeds (Beveridge 1964; Daniel 1973), and brushtail possums commonly eat the flesh from the fruits and drop the seeds undispersed below the parent tree (Cowan and Waddington 1990). Consequently, hīnau could be suffering from dispersal limitation across most of the mainland where mammalian seed predators are common and few of its dispersers occur.

Conservation efforts in New Zealand have eradicated exotic mammals from many offshore islands and fenced sanctuaries (Towns and Broome 2003; Parkes et al. 2017), bolstering frugivore populations (Murphy and Kelly 2001; Graham and Veitch 2002;

Graham et al. 2013; Iles and Kelly 2014) and restoring a more intact ecosystem (Saunders and Norton 2001; Tanentzap and Lloyd 2017). For example, endemic bellbird (*Anthornis melanura*) densities on the Poor Knights Islands (a sanctuary that has never been invaded by exotic mammals) are 54 times greater than average densities on the New Zealand mainland (North and South Islands) (Bartle and Sagar 1987). These islands offer the opportunity for testing the influence of native dispersers and exotic mammals on seed dispersal rates through comparisons between island avifaunas with high bird densities and bird species of restricted distributions (Iles 2012; Graham et al. 2013) and depauperate mainland sites. I used replicated, paired mainland and island sanctuary sites to assess whether hīnau is dispersal limited on the mainland and whether it appears adapted for dispersal by flightless birds such as weka. I also used these sites to assess seed predation rates by exotic mammals. Specifically, I aimed to answer the following questions:

1) What proportion of hīnau fruits are handled by frugivores in the canopy (the percentage of fruits captured below trees that have passed through a bird; an index of dispersal quantity), and does this proportion vary with abundance of volant frugivores?

2) What proportion of hīnau fruits which reach the ground is dispersed from there, and does that vary between predator-free island sanctuaries and mainland sites?

3) What species of frugivore remove hīnau fruits from the ground, and how important among these are weka?

4) What levels of seed predation does hīnau experience, and are seed predation rates lower on predator-free islands than on the mainland?

4.3 Methods

4.3.1 Study species

Hīnau is a lowland forest tree that occurs across the North Island and the West Coast of the South Island. Its fruits are oval purple-brown drupes measuring 9.2 mm

diameter on average (Kelly et al. 2010), with a high percentage of flesh (the mesocarp, 25% by mass) and a relatively low water content (66%; Williams 1982). The seed is protected inside a hard, thick seed coat (the endocarp) so that rodents can only destroy the ripe seeds by gnawing through the seed coat (Fig. 4.1a; Beveridge 1964, Daniel 1973), though kākā *Nestor meridionalis* (an endemic parrot) split the seed coat while it is still green and consume the developing seed (Moorhouse 1997). Fruit crop size is variable from year to year, ranging from less than 1000 to more than 30,000 fruits per tree (Cowan and Waddington 1990). Hīnau's seedfall coefficient of variation is 0.83, which defines it as a moderately masting species when compared to other New Zealand plants (Webb and Kelly, 1993; Kelly and Sork, 2002; Kelly et al., 2013). Fruits ripen and fall between March and September.

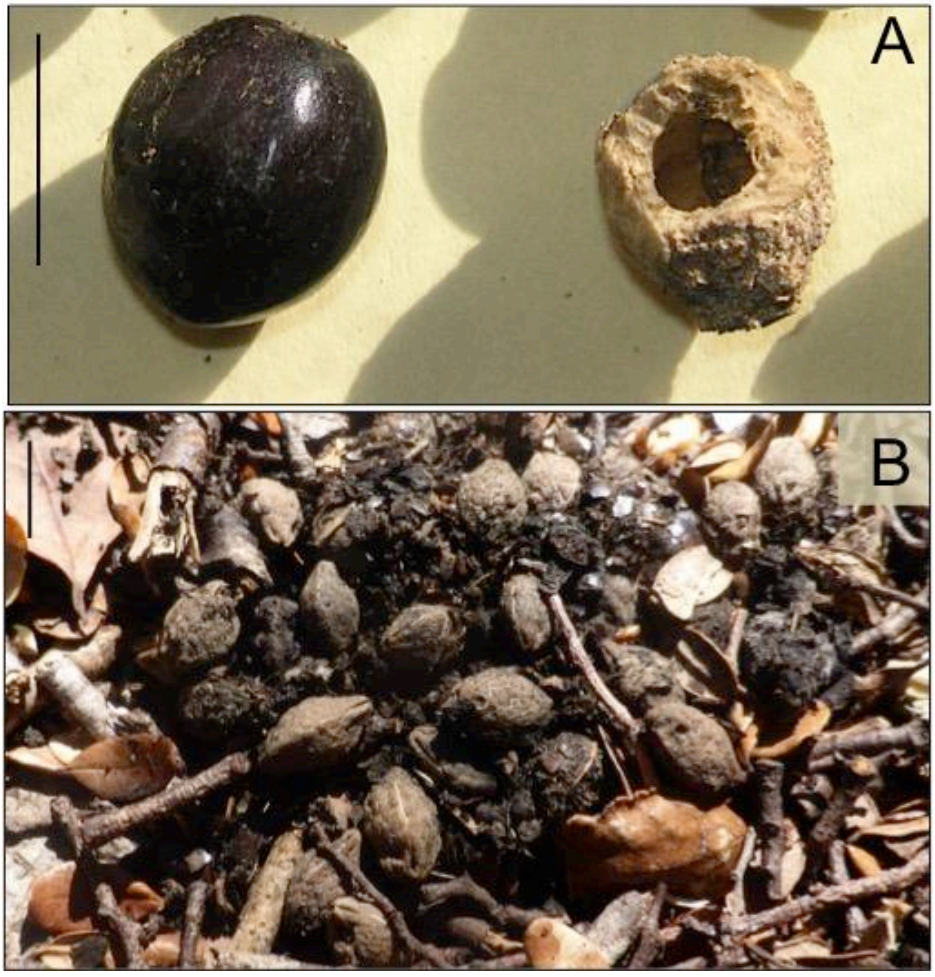


Fig. 4.1. *A) Photo depicting a whole, ripe hīnau fruit on the left, and a rat destroyed hīnau seed on the right. B) Photo of weka faeces on D'Urville Island containing >13 whole hīnau seeds, courtesy of Geoff Walls. Scale bars are 10 mm.*

4.3.2 Sites

Monitoring occurred at two island/mainland pairs located in central New Zealand: one pair in the upper South Island (Blumine Island/Oruawairua -41°17’ 47 S, 174°24’ 10 E, and Essons Valley 41°30’ 46 S, 174°00’ 94 E), and one pair in the lower North Island (Kapiti Island -40°85’ 18 S, 174°91’ 41 E, and Catchpool Valley -41°35’ 10 S, 174°92’ 57 E) (Fig. 4.2). Kapiti Island is approximately 54 km from Catchpool Valley, and Blumine Island is approximately 23 km from Essons Valley. The two islands have high levels of native frugivorous birds such as weka, kererū, tūī *Prosthemadera novaeseelandiae*, and bellbirds, as well as frugivores now rare or absent from the mainland (tīeke *Philesturnus carunculatus*, kiwi *Apteryx* spp., kākā, and kākāriki *Cyanoramphus* spp.) (Robertson et al. 2007). The mainland sites contain a suite of introduced mammalian species including brushtail possums, ship rats, Norway rats, house mice, and feral pigs, which are absent from the island sites (King 2005). As a result, they have lower numbers of native frugivorous birds such as kererū, tūī, and bellbirds (Murphy and Kelly 2001; Robertson et al. 2007; Iles and Kelly 2014). Essons Valley has low numbers of weka (Pers. Obs.) but Catchpool has none (Robertson et al. 2007).

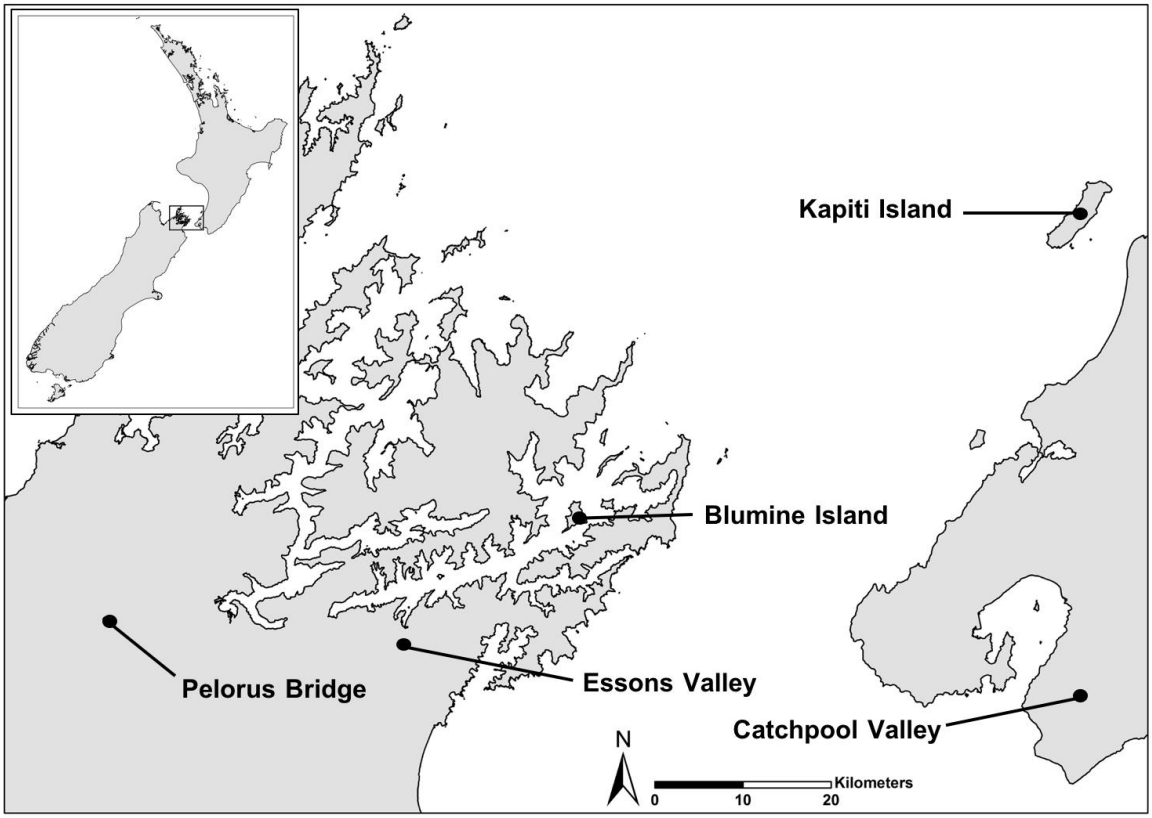


***Fig. 4.2**. Map showing the paired, mainland-island sites, and their location in wider New Zealand (inset). Blumine Island and Essons Valley are the South Island pair, while Kapiti Island and Catchpool Valley are the North Island pair. Fruit handling indices from seed traps at Pelorus Bridge were used as a surrogate for Essons Valley, where seed traps were not established.*

4.3.3 Indices of dispersal and seed predation from the canopy

Seed traps were established beneath the canopies of ten hīnau trees per site on Kapiti Island, Blumine, and Catchpool Valley to obtain fruit handling and seed predation indices from the canopy. Fruit handling indices were comprised of the proportion of seeds captured that had passed through a bird, and seed predation indices were comprised of the proportion of seeds captured that had been destroyed. Each seed trap was comprised of a 41 cm x 29 cm x 6.2 cm plastic seed raising tray, covered with plastic mesh to discourage fruit removal from the traps, and pegged securely to the ground. Two traps were set up beneath each tree, giving a catching area of 0.24 m^2 per tree. Seed traps were established in March or April 2017 and were checked monthly until September 2017 (the end of the hīnau fruiting season). Fruits were classed as

either: passed through a frugivore (fruit skin removed but no visible chew damage), preyed on by native parrots (endocarp cleaved in half, destroying the seed inside), chewed by possums (exocarp and mesocarp removed with chew marks), or intact whole fruits found under parent trees (both ripe and unripe). Fruits that had passed through a frugivore were distinguished by their slippery texture, with some mesocarp remaining on the seed (Carpenter et al. 2017). Further seed trap data were obtained from the Department of Conservation's national seed rain monitoring network, which gave fruit handling indices from an additional mainland site at Pelorus Bridge (Marlborough), about 35 km west of Essons Valley. The fruit handling data obtained from seed traps at this site were used as a surrogate for Essons Valley, where no seed traps were established. Pelorus Bridge used elevated conical seed traps with a catching area of 0.28m^2; see Carpenter et al. (2017) for a description. Kererū, bellbirds, and tūī occurred in low numbers at this site (Robertson et al. 2007; Carpenter et al. 2017). Rodents and possums were also present.

4.3.4 Canopy visitation rates

Between April and June eight trail cameras were each trained on a fruiting branch in the canopy of a hīnau tree across three of the sites (one on Kapiti Island, three at Catchpool Valley, and four on Blumine Island). As these trees needed to have suitable low-hanging branches, different trees were selected from the trees that had seed traps and ground cameras below them. Cameras were mounted on the top of 5.5 m telescopic poles, secured with guy lines and pegs. Cameras were set on motion detect photographic mode to obtain images of volant bird visitation rates over two weeks at each site. The five cameras on Blumine Island were left for an additional three weeks monitoring to maximise the chance of recording volant frugivores.

4.3.5 Fruit removal and destruction rates on the ground

Motion-triggered video camera traps were used to positively identify species that dispersed or destroyed deposits of hīnau seeds that I placed on the forest floor. Seeds that were removed by rodents or pigs were classed as depredated. Ship rats, Norway rats, Polynesian rats, and mice remove seeds for consumption at safe, sheltered sites, but they do not display scatterhoarding behaviour (burying seeds in widely spaced

caches), and hīnau seeds are too large for them to swallow and disperse intact. Instead, rodents destroy hīnau seeds by gnawing through the seed coat (Beveridge 1964, Grant-Hoffman & Barboza 2010, Daniel 1973). Pigs eat and crush whole hīnau fruits, with pig guts containing large quantities of destroyed hīnau seeds (Beveridge 1964). Fruits that were removed by weka or kererū were classed as dispersed as these species swallow the fruits and defecate the seeds intact (Fig. 4.1b; Geoff Walls pers. comm.; Beauchamp 1987, Kelly *et al.* 2010).

One trail camera (either a LTL Acorn 5310A Wide Angle Trail & Security Camera, KeepGuard KG690NV 8MP Wildlife Camera, or Moultrie Game Spy M-990i Gen 2 10.0 MP Camera) was placed 50 – 200 cm in front of a depot of ripe hīnau fruit beneath the canopy of each of ten fruiting hīnau trees per site. These were the same trees that had seed traps below them at Kapiti Island, Blumine Island, and Catchpool Valley. Cameras were mounted about 1 m above the ground. Ten ripe fallen fruits were placed in a small depression on the ground cleared of leaf litter and debris (Moles and Drake 1999). For trees that did not have enough fallen fruit beneath them to create a depot of monitored fruits I used fruits from nearby trees. Where mammals were present, fruits were handled using latex gloves rinsed in water to avoid affecting disperser behaviour with human scent (Wenny 2002). The number of fruits dispersed or preyed upon was recorded after two, nine, and fourteen days, and then the cameras were removed. Hīnau fruits remain fresh for many weeks on the ground (Pers. Obs.), and were still in excellent condition when monitoring finished. Camera footage was used to identify the animal species that interacted with fruits. Monitoring occurred between April and June 2017 (the peak of the hīnau fruiting season).

4.3.6 Statistical analysis

I used binomial generalised linear mixed effects models (GLMMs) in a classical framework to assess whether fruit handling rates from the canopy differed between islands and the mainland, and whether fruit removal by dispersers from the ground differed between island and mainland sites. For the fruit handling rates from the canopy model, the proportion of fruits per trap per year (March – September) that had passed through a bird was the response variable, site status (mainland or island) was

the fixed effect, and site was the random effect. For the ground dispersal model, proportion of all fruit in the depot removed by legitimate dispersers (weka, kererū) was the response variable, site status was the fixed effect and site was a random effect. I corrected for overdispersion in this model using an observation level random effect (Browne et al. 2005).

In order to assess the importance of various dispersers and seed predators, I used Bayesian statistics (Ellison 2004) to test for differences among ground-based frugivores in the mean percentage of hīnau fruit they removed. I was interested in determining the probability that a seed placed onto the forest floor would be removed by each of the species present at a site. Frugivore species were only included as present at a site if they were detected on the ground by a camera and had removed a fruit at one of the sites. Using these criteria, Blumine had weka and kererū, Kapiti had only weka, Essons had weka, rats, mice, and pigs, and Catchpool had rats and mice. I fitted a mixed effects logistic multinomial regression model using the Deviance Information Criterion (DIC) to select the best statistical model (Spiegelhalter et al. 2002). Our response variable was a vector consisting of the number of seeds removed by each frugivore type, with site and camera ID included as random effects. I used the statistical software package WinBUGS (Spiegelhalter et al. 2002) for our analysis and the software R (R Development Core Team 2010) for additional posterior probabilities.

4.4 Results

4.4.1 Hīnau dispersal

Seed trap data from all sites showed that there was no significant difference between canopy dispersal rates (proportion of seeds in seed traps that had been through a frugivore) on the mainland (Catchpool Valley and Pelorus) compared to the islands (Blumine Island and Kapiti Island; $Z = -1.642$, $p = 0.10$). Low levels of dispersal occurred at all four sites (mean of 13.7% canopy seeds dispersed for islands [41 of 278 captured seeds] and 2% on the mainland [14 of 514 captured seeds]; Fig. 4.3). Thus, canopy dispersal of hīnau fruit was uncommon even on islands with high abundances of endemic birds.

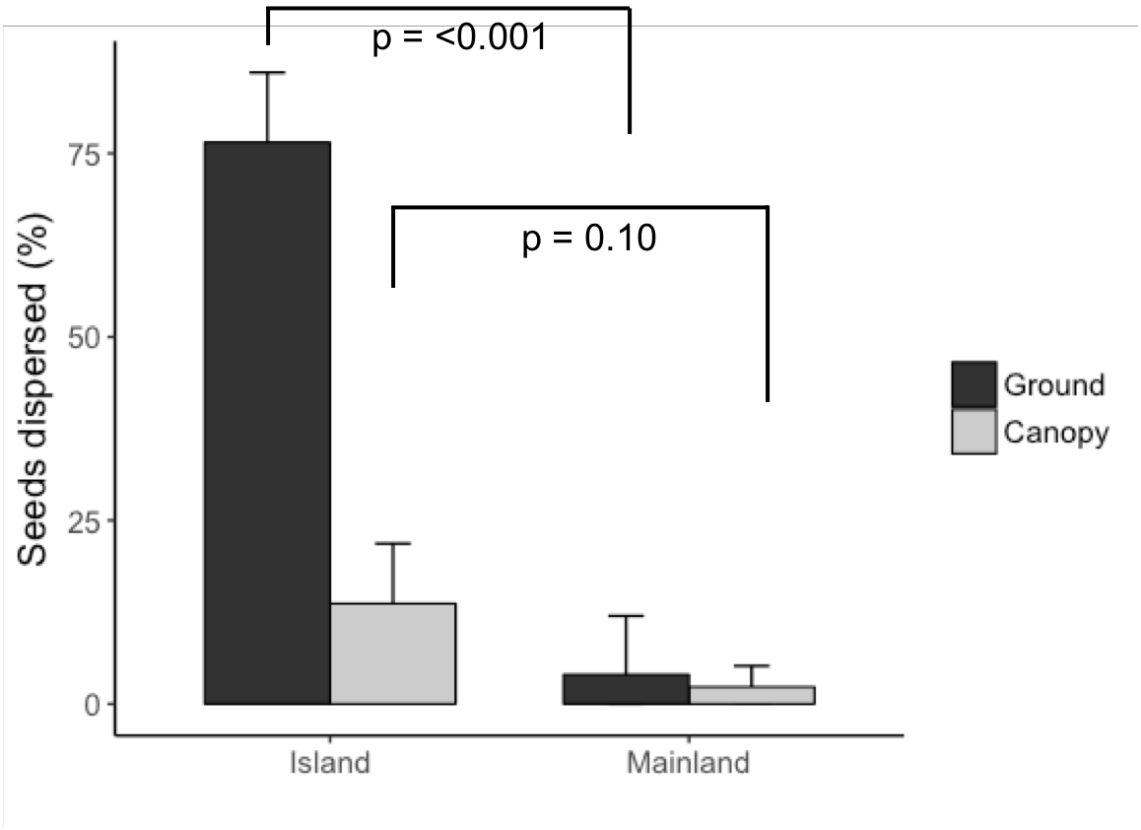


Fig 4. Mean percentage of seeds consumed by dispersers (ground seed data from camera traps) or passed through a bird (canopy seed data from seed traps) for island (n = 2 sites) and mainland sites (n = 2 sites). Error bars are bootstrapped 95% confidence intervals.

The four canopy cameras on Blumine Island provided between 6 to 36 days of usable footage each. The camera on Kapiti Island provided 14 days of footage, and the three cameras at Catchpool each provided 14 days of footage. This added up to 42 days footage from the mainland site, and 124 days footage from the two island sanctuary sites. No frugivorous birds visited the tree canopies at Catchpool over the two weeks of monitoring, although possums were recorded. Five visits from kererū and two from tūī were recorded on Blumine. A single visit by a kākā was recorded on Kapiti Island. As the cameras were set to take photos rather than video footage, fruit consumption by each individual bird was not assessed. There was not enough data to analyse canopy visitations, but these preliminary results show that few birds visited hīnau canopies even on islands with high numbers of birds.

Hīnau seeds on the ground were far more likely to be dispersed on islands (76.5% of seeds dispersed; 153 out of 200 monitored seeds), than at the two mainland sites (4%; 8 out of 200 monitored seeds from Catchpool Valley and Essons Valley). Site status was a significant effect in our GLMM ($Z = -5.489$, $p = <0.001$; Fig. 4.3). Weka and kererū were the only two dispersers recorded consuming fruits from ground depots. Blackbirds (*Turdus merula*), song thrushes (*Turdus philomelos*), tīeke, robins (*Petroica* spp.), and little spotted kiwi (*Apteryx owenii*) were all detected by cameras but were not seen to consume any fruit. The Bayesian probability analysis found that weka were the most likely species to consume hīnau fruits off the ground on island sanctuaries (Fig. 5; likelihood of weka removing a fruit rather than other species on islands >0.9999). Weka faeces filled with hīnau seeds were a common sight on Blumine Island in particular. In summary, I recorded high proportions of hīnau seeds on the ground being dispersed (predominantly by weka) on islands, with much lower dispersal levels at mainland sites.

4.4.2 Hīnau seed predation

No seeds on the ground were destroyed at the two island sites (0 out of 200 monitored seeds), but 21.5% seeds (43 out of 200 monitored seeds) were removed by rodents or pigs (and therefore assumed to be destroyed) at the two mainland sites (Catchpool Valley and Essons Valley). Rodents were the most likely taxon to remove a seed from the ground at the mainland sites (Fig 4.4; probability of a rodent removing a fruit compared to other species present at the sites = 0.9 and 0.99 for Catchpool and Essons Valley respectively). Possums had chewed an average of 55% of fruits on the ground (110 out of 200 monitored seeds) at the two mainland sites but did not destroy or remove any seeds. However, possum handling of fruits might have a small negative effect by reducing fruit attractiveness to legitimate dispersers (see Discussion).

Data from the seed traps showed that over the entire fruiting season, endemic parrots destroyed 32.5% of the seeds from the canopy at the two island sites (90.5 out of 278 captured seeds). No seeds were destroyed from the canopy at Catchpool Valley, although possums in the canopy had chewed 91.7% (364 out of 397 captured seeds) of seeds captured in seed traps at this site. In summary, exotic seed predators removed

and likely destroyed 21.5% of seeds on the ground at the mainland sites in two weeks, while no seeds were destroyed on the ground on island sanctuaries. However, endemic parrots on islands destroyed 32.5% of seeds from the canopy over the entire fruiting season (~6 months).

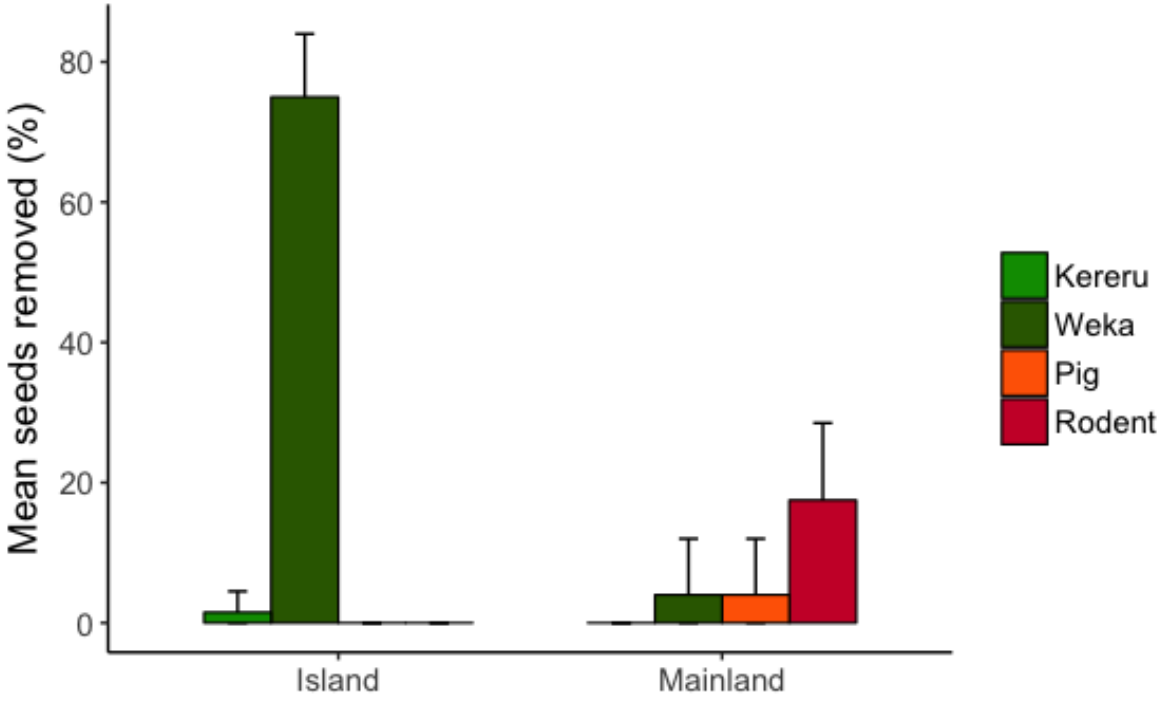


Fig. 4.4. *Mean percentage of ground fruits removed by each species across island and mainland sites. Green colours denote endemic seed dispersers, red colours denote exotic seed predators. Error bars are bootstrapped 95% confidence intervals.*

4.4.3 Possible combined impact of seed predation and dispersal

Using the figures above, I present one possible integration of the effects of hīnau seed predation and dispersal on the mainland compared to island sanctuaries over an entire fruiting season. It is important to note that this integrative approach uses figures obtained from a range of different methods and is therefore speculative. This composite summary (Fig. 4.5) follows the sequential fate of 100 seeds on both sanctuary islands and the mainland, using the percentages of seeds that were dispersed or destroyed at each stage (canopy and ground). The results of this summary demonstrate that on islands, 32.5% of hīnau seeds are destroyed, 53.8% are dispersed,

and 13.7% are undispersed. On the mainland, 42.1% of seeds are destroyed, 5.9% are dispersed, and 51.9% are undispersed. The key finding is that on sanctuary islands most undestroyed hīnau seeds are dispersed, while on the mainland they remain undispersed beneath the parent tree.

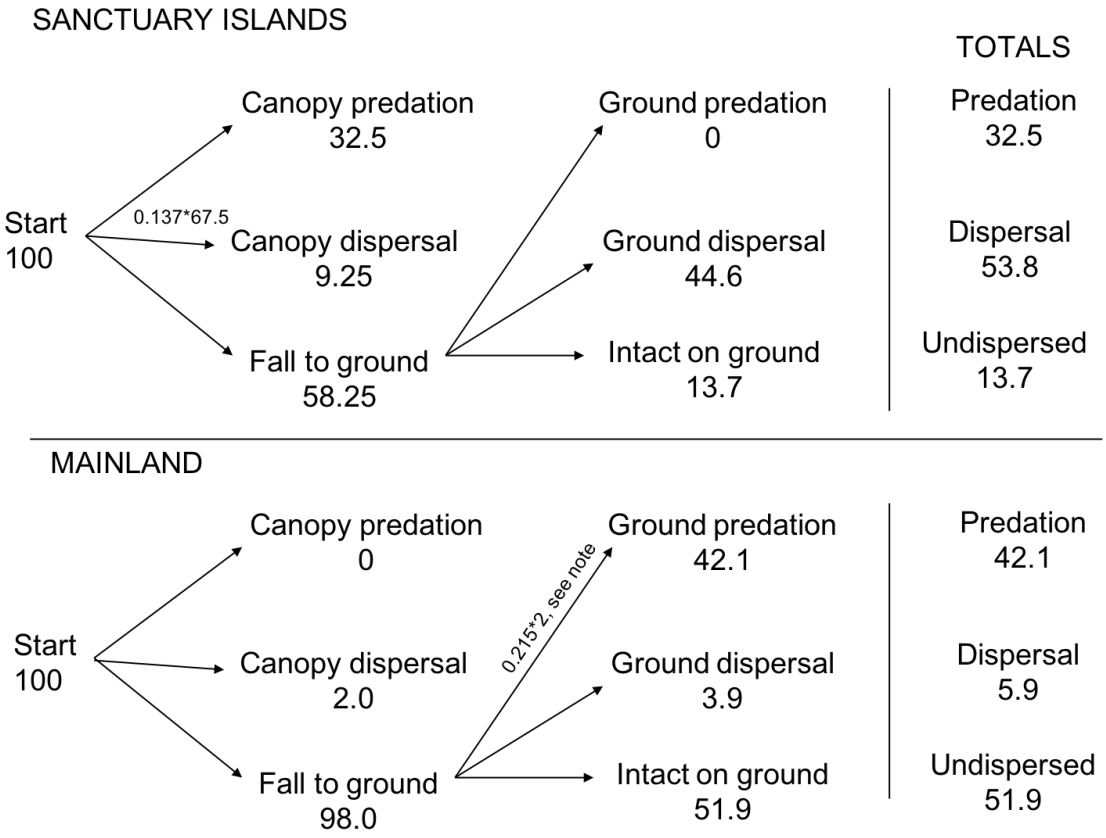


Fig. 4.5. *Flow chart showing one possible integration of the effects of seed predation and dispersal on sanctuary islands and the mainland over an entire fruiting season. The chart starts with 100 seeds at each location type (sanctuary islands vs. mainland) and plots their sequential fates, using percentages of seed predation and dispersal obtained from camera traps and seed traps. This integrative approach uses figures obtained from a range of different methods and is therefore speculative. Note: For the purposes of this composite summary, I have assumed the percentage of seed predation by exotic mammals that I recorded over two weeks (21.5%) would double if I had measured for an entire 6 month fruiting season (see Discussion). Therefore I have assumed a predation rate of 43% for this composite summary.*

I made several assumptions when calculating this possible integration of seed predation and dispersal. As mammalian predation from the ground was only measured for two weeks, I assumed that this rate of predation would double if I had measured for the entire 6 month fruiting season (see discussion), so I have used a mammalian predation rate of 43%. While this rate is very speculative, it correlates well with the rate of mammalian predation on hīnau seeds recorded by other studies (Overdyck et al. 2013). I also assumed that parrot seed predation was on green fruit only (as the endocarp of ripe fruit is too hard for parrots to destroy; Moorhouse, 1997), therefore removing fruits from the potential dispersal pool before they could be dispersed. Finally, for the purpose of this summary I assumed that fruits that were dispersed from the canopy were not vulnerable to ground predation (as the flesh from the fruit is removed, making the fruits unattractive to seed predators).

4.5 Discussion

I found that hīnau had significantly less dispersal from the ground at mainland sites where native frugivores have declined or gone locally extinct compared to island sanctuaries that more closely approximate pre-human frugivore communities. On sanctuary islands where weka were abundant, the majority of seeds that fell to the ground were consumed and dispersed by weka, while on the mainland the majority of seeds on the ground were chewed by possums and left in situ. Most of the remaining seeds on the ground at mainland sites were removed, and likely destroyed, by exotic seed predators such as rodents and pigs. As I expected, dispersal rates from the canopy were poor at both island and mainland sites, possibly because hīnau fruit fall to the ground when ripe rather than being retained in the canopy. This is consistent with kererū being observed consuming fruit both in the canopy and from the ground. All this suggests that hīnau is adapted for dispersal by flightless birds (discussed further below).

Several other studies have demonstrated that frugivore declines caused by invasive species can have cascading effects on seed dispersal services. In New Zealand, *Pittosporum crassifolium* experienced poor seed dispersal (20% of seeds removed by birds) at mainland sites compared to sanctuary island Tiritiri Matangi Island (94%

removal) (Anderson et al. 2006), and nikau *Rhopalostylis sapida* and *Fuchsia excorticata* also have impaired dispersal on the mainland compared to Kapiti Island (McNutt 1998). Tawa *Beilschmiedia tawa* also appears to suffer from extremely low dispersal at some mainland sites (<10% of seeds captured below parent canopies had passed through a bird at three North Island sites; Silberbauer 2013), although eight other studies on seed dispersal quantity in mainland New Zealand have found adequate dispersal rates (Kelly et al. 2010; Pegman et al. 2017). On the Balearic Islands, introduced carnivorous mammals have indirectly lowered seedling recruitment of a perennial shrub by driving its mutualistic partner extinct (Traveset and Riera 2005), while on Guam the near-total loss of frugivorous birds caused by the exotic brown tree snake (*Boiga irregularis*) may have caused a 61 – 92% decline in seedling recruitment for two plant species (Rogers et al. 2017) and a reduction in seedlings of all tree species reaching canopy gaps away from parent trees (Wandrag et al. 2017). Whether the reduced dispersal I have recorded results in lowered recruitment for hīnau depends on hīnau's reliance on avian dispersal for improved germination (e.g. by gut passage, see Robertson *et al.* 2006) and escape from disproportionate density- and distance- dependent mortality beneath parent canopies (i.e. Janzen-Connell effects, see Comita *et al.* 2014). A New Zealand study on two other large-fruited native trees (*Corynocarpus laevigatus* and *Beilschmiedia tarairi*) found better recruitment to the 2-year-old seedling stage away from parents of both species, suggesting that frugivore declines would reduce regeneration (Wotton and Kelly 2011). Carpenter et al. (2018) demonstrated that simulated avian gut passage may increase the germinability of hīnau compared to whole fruits, so the results I have shown could have flow-on effects to recruitment. Further research is needed to examine hīnau's susceptibility to Janzen-Connell effects.

4.5.1 The importance of weka

Weka have disappeared from most regions of the North and South Islands since 1900 and some subspecies are threatened (Robertson et al. 2007), but weka can be a controversial species in New Zealand conservation because of their predatory impacts on native fauna, including birds (Harper 2006), herpetofauna (Lettink. et al. 2010), and invertebrates (Gibbs 2010). At times, this has resulted in their exclusion from mainland

restoration projects, even in areas where they historically occurred (Miskelly and Beauchamp 2004). Importantly, this study has highlighted the positive ecosystem services that they also provide, with weka dispersing the majority of hīnau fruits from the ground on island sanctuaries. Given that the low fruit handling rates I recorded from the canopy suggested hīnau is not regularly dispersed by volant birds, weka appear to be the primary disperser for hīnau where they are present. This is concerning given that weka are now extinct over large tracts of their historic range (including most of the range of hīnau) due to a combination of mammalian predation, habitat loss, and possible drought-induced starvation (Miskelly and Beauchamp 2004). Their susceptibility to rapid population declines makes conservation action even more pressing (Beauchamp et al. 1999).

In addition to hīnau, weka have also been recorded consuming the fruits of a wide range of other plants, including *Geniostoma ligustrifolium* var. *ligustrifolium*, *Coprosma* spp., *Passiflora tetrandra*, *Piper excelsum*, *Pseudopanax arboreus*, *Prumnopitys ferruginea, Carpodetus serratus,* and *Pennantia corymbosa* (Coleman et al. 1983; Beauchamp 1987). Several weka dietary studies have recorded weka eating large amounts of fruit in certain seasons (Coleman et al. 1983; Beauchamp 1987), so the seed dispersal services these birds provide for other plant species could be considerable. However, effective seed dispersal includes both dispersal quantity (the number of seeds dispersed) and dispersal quality (the treatment of seeds in the mouth and gut, and the locations of seed deposition) (Schupp et al. 2010). While weka provided good dispersal quantity for hīnau, further research is required to assess the quality of dispersal they provide. Mechanical scarification of the seedcoat has been shown to increase the germinability of hīnau seeds (Carpenter et al. 2018), and it is possible that the grit within weka gizzards (Carroll 1963) may abrade hīnau seeds during gut passage in a similarly beneficial way. Germination trials using weka-passed seeds from a wide range of plant species would be useful. Similarly, mechanistic models that combined both gut passage times and high-resolution movement patterns for weka would further clarify their seed dispersal capabilities.

4.5.2 The importance of ground dispersal

My findings strongly suggest that hīnau fruits were primarily dispersed by flightless birds in pre-human New Zealand. I recorded high levels of fruit removal from the ground on islands that retain much of their pre-human avifauna, and fruit handling rates from the canopy on islands were still poor despite higher numbers of volant frugivores. While fruit handling rates do not provide information on quantitative seed dispersal (as successful seed dispersal typically requires the movement of fruits away from beneath parent tree canopies), fruit handling rates are monotonically related to the percentage of seeds that are moved away from beneath the parent canopy and therefore they are an index of dispersal quantity (Wyman 2013). The fruit handling rates I recorded are therefore probably lower than the actual dispersal rate, although they are likely to also include seeds that have been consumed at other hīnau trees and dispersed away from the parent canopy. Although it is difficult to objectively define what constitutes 'poor' fruit handling rates, the indices I recorded here are lower than those found for other New Zealand native fruiting trees (such as miro *Prumnopitys ferruginea*, matai *Prumnopitys taxifolia*, rimu *Dacrydium cupressinum*, and kahikatea *Dacrycarpus dacrydioides*; Carpenter et al. 2017) that are dispersed by smaller still-widespread frugivores. In addition, I found very low avian visitation rates to hīnau canopies, both on the mainland and on island sanctuaries, which suggests that hīnau is not very attractive to volant dispersers.

While I recorded reasonably high levels of fruit removal from the ground on sanctuary islands, pre-human levels of ground fruit removal could have been even higher. There would have been far richer species diversity and greater abundances of flightless birds in New Zealand's pre-human ecosystems (potentially >27 species; Atkinson and Millener 1991), and even if their diets were not primarily frugivorous these flightless birds would have likely moved many seeds due to their sheer abundance (Lord 2002). Furthermore, even volant frugivorous birds probably spent more time foraging on the ground prior to the arrival of mammalian predators (Wotton 2007). Kererū, tīeke, and kākāriki are frequently seen feeding on the ground on islands that are free of mammalian predators (Wotton 2007; Innes et al. 2010), and I recorded kererū consuming hīnau fruits from the ground on Blumine Island.

This study is the first report of high levels of seed dispersal by a flightless bird in New Zealand. Cassowaries and emus are key seed dispersers for many plant species in Australia, consuming a wide variety of seeds and moving them large distances (e.g. Calviño-Cancela et al. 2006, Bradford & Westcott 2010). Taken together, these results suggest that ground removal of fruit by flightless birds may be or has been an important dispersal mechanism in other parts of the world. Flightless birds are common on oceanic islands that lack mammalian predators, but such birds have frequently undergone severe declines or extinctions since human arrival. Duncan et al. (2013) demonstrated that across the Pacific, flightless birds were 33 times more likely to have gone extinct than volant birds. For example, Hawai'i harboured at least 20 species of flightless birds before human arrival, including 12 rails (Olson and James 1991). Greater Polynesia has also suffered from major losses of ground-dwelling birds, with Steadman (1995) estimating that "flightless rails alone may account for 2000 species of [extinct] birds that would have been alive today had people not colonized Oceania". Dispersal may be reduced if these birds historically performed seed dispersal services, but their possible contributions are rarely examined or considered. Megapodes (*Megapodius spp*.), for example, may be significant seed dispersers, but this has never been investigated and many species from this genus are now extinct (Meehan et al. 2002).

4.5.3 Seed predation

Exotic rodents were the most common species to remove and presumably destroy seeds at mainland sites, while no seeds were destroyed on the ground on the islands. Similarly, Overdyck *et al.* (2013) recorded ~40% of hīnau seed being removed by exotic rodents in an urban forest remnant after three weeks, and Daniel (1973) recorded ship rats destroying 21% of hīnau seeds under parent trees. The rodents now in New Zealand (mice, ship rats, Norway rats, and Polynesian rats) do not display scatterhoarding behaviour (i.e. burying seeds in widely-spaced caches; Vander Wall 1990), which is the typical mechanism of seed dispersal by rodents in the Northern Hemisphere. Instead, these taxa display caching behaviour (Williams et al. 2000; Morriss et al. 2012), where they carry seeds away for consumption at sites where they are safe from predators, competitors, and rain. Previous research suggests that the

majority of cached hīnau seeds end up destroyed. On Tiritiri Matangi Island, 62% of hīnau seeds found in Polynesian rats' 'husking stations' were destroyed (Campbell et al. 1984), while Beveridge (1964) recorded finding "piles of [rodent] gnawed miro and hīnau seed … under logs and in other sheltered positions in the forest." Mice have also been discovered caching hīnau seeds in plastic tunnels that are intermittently used as bait stations, with most seeds destroyed (J. Ledington pers. comm. 2017). Because the seeds are not buried, and cache sites are typically sheltered, dark, dry places, uneaten seeds have little chance of establishing. For example, Polynesian rats cache seeds in tree roots, fissures in tree trunks, amongst rock piles, and occasionally up trees (Campbell et al. 1984). Similarly, exotic rats in Hawai'i moved a large proportion of palm seeds up to 8 metres away from their collection site and subsequently destroyed them (Shiels and Drake 2015).

I also assumed that the majority of seeds consumed by feral pigs were destroyed. Large quantities of destroyed hīnau seeds have been reported in the guts of feral pigs (Beveridge 1964), and O'Connor and Kelly (2012) found that feral pigs passed intact only 14% of New Zealand matai seeds (*Prumnopitys taxifolia*). Matai seeds are only slightly smaller than hīnau with a similar hard, woody endocarp so I anticipate that the survival rates are probably similar. While I recorded only low numbers of pigs removing hīnau seeds, this probably reflects low pig densities rather than dietary preferences. In New Zealand, feral pigs have a patchy distribution and can range widely to forage on preferred foods, so local pig densities vary greatly in space and time (King 2005). Hīnau seeds are a popular food choice for pigs, making up 30.9% of their diet in combination with tawa *Beilschmiedia tawa* at a North Island site (Thomson and Challies 1988).

Endemic parrots (kākā and kākāriki) destroyed 32.5% of seeds from the canopy at the island sites over an entire 6 month fruiting season. Kākā are formidable seed predators and have been recorded destroying an average of 7.1 hīnau seeds per minute on Kapiti Island (Moorhouse 1997). In the early stages of human settlement kākā were extremely abundant and the impact of their seed predation on favoured tree species was probably immense. Hīnau's highly variable crops may therefore have evolved to satiate parrot seed predators during heavy fruiting years, enabling a proportion of the crop to survive (Kelly and Sork 2002; Koenig et al. 2003). While the seed predation

rates I recorded for endemic parrots appear higher than those recorded for exotic mammals on the mainland (21.5%), it is important to note that I cannot directly compare these two measures of seed predation as they use different monitoring methods (seed traps vs. camera footage) over different timespans (6 months for parrots vs. 2 weeks for mammals). However, it seems likely the proportion of seeds destroyed by exotic mammals would have increased if I had monitored over the entire season. For example, Overdyck et al. (2013) observed that the proportion of hīnau fruit removed by exotic mammals continued to increase over 50 weeks, although the rate of seed removal slowed after three weeks.

Finally, I recorded possums chewing large proportions of hīnau seeds both on the ground and in the canopy at mainland sites. While these interactions did not destroy the hīnau seeds, the removal of the carbohydrate-rich mesocarp may make these seeds less attractive to legitimate dispersers. In addition, possums negatively affect hīnau recruitment by consuming hīnau flowers and significantly supressing fruit production (Cowan and Waddington 1990), so their impact on the tree is largely deleterious.

4.5.4 Conclusions

I found that ground based dispersal of hīnau is impaired on the New Zealand mainland compared to sanctuary islands, due to low frugivore numbers. Seeds on the ground at mainland sites were most likely to be removed by exotic seed predators, while seeds on the ground on island sanctuaries were most likely to be removed by endemic seed dispersers. This study has also highlighted the importance of an unexpected disperser for hīnau, the charismatic but controversial weka. This finding demonstrates the importance of testing which species perform important mutualistic services, rather than simply relying on logical assumptions. In future, conservation management decisions regarding the removal (or non-reintroduction) of weka in restoration projects should carefully consider the seed dispersal services they provide. Further research is needed to assess whether the reduced dispersal I observed is reducing recruitment.

4.6 References

Anderson S, Kelly D, Robertson A, et al (2006) Birds as pollinators and dispersers: A case study from New Zealand. Acta Zool Sin 52:112–115

Atkinson IAE, Millener PR (1991) An ornithological glimpse into New Zealand's pre-human past. Proc 20th Int Ornithol Congr 1:129–192

Bartle J, Sagar P (1987) Intraspecific variation in the New Zealand bellbird Anthornis melanura. Notornis 34:253–306

Beauchamp A (1987) A population study of the weka, Gallirallus australis, on Kapiti Island. Victoria University of Wellington

Beauchamp AJ, Butler DJ, King D (1999) Weka (Gallirallus australis) recovery plan 1999-2009. Threatened Species Recovery Plan 29.

Beveridge AE (1964) Dispersal and destruction of seed in central North Island podocarp forest. Proc New Zeal Ecol Soc 11:48–55

Bradford MG, Westcott DA (2010) Consequences of southern cassowary (Casuarius casuarius, L.) gut passage and deposition pattern on the germination of rainforest seeds. Austral Ecol 35:325–333 . doi: 10.1111/j.1442-9993.2009.02041.x

Browne WJ, Subramanian S V., Jones K, Goldstein H (2005) Variance partitioning in multilevel logistic models that exhibit overdispersion. J R Stat Soc Ser A Stat Soc 168:599–613 . doi: 10.1111/j.1467-985X.2004.00365.x

Calviño-Cancela AM, Dunn RR, Etten EJB Van, et al (2006) Emus as non-standard seed dispersers and their potential for long-distance dispersal. Ecography (Cop) 29:632–640

Calviño-Cancela M (2002) Spatial patterns of seed dispersal and seedling recruitment in Corema album (Empetraceae): The importance of unspecialized dispersers for regeneration. J Ecol 90:775–784 . doi: 10.1046/j.1365-2745.2002.00711.x

Campbell DJ, Atkinson IAE (2002) Depression of tree recruitment by the Pacific rat (Rattus exulans Peale) on New Zealand's northern offshore islands. Biol Conserv 107:19–35 . doi: 10.1016/S0006-3207(02)00039-3

Campbell DJ, Moller H, Ramsay GW, Watt JC (1984) Observations on foods of kiore (Rattus exulans) found in husking stations on northern offshore islands of New Zealand. N. Z. J. Ecol. 7:131–138

Carpenter JK, Kelly D, Clout MN, et al (2017) Trends in the detections of a large frugivore

(Hemiphaga novaeseelandiae) and fleshy-fruited seed dispersal over three decades. N Z J Ecol 41:41–46 . doi: 10.20417/nzjecol.41.17

Carpenter JK, Wood JR, Wilmshurst JM, Kelly D (2018) An avian seed dispersal paradox: New Zealand's extinct megafaunal birds did not disperse large seeds. Proc R Soc B Biol Sci 285: . doi: 10.1098/rspb.2018.0352

Carroll ALK (1963) Food habits of the North Island weka. Notornis 10:289–300

Christian CE (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. Nature 413:635–639 . doi: 10.1038/35098093

Clout MN, Hay JR (1989) The Importance of Birds As Browsers, Pollinators and Seed Dispersers in New Zealand Forests. N Z J Ecol 27–33 . doi: 10.2307/24053245

Clout MN, Karl BJ, Pierce RJ, Robertson HA (1995) Breeding and survival of New Zealand Pigeons Hemiphaga novaeseelandiae. Ibis (Lond 1859) 137:264–271 . doi: 10.1111/j.1474-919X.1995.tb03248.x

Coleman JD, Warburton B, Green WQ (1983) Some population statistics and movements of the western weka. Notornis 30:93–107

Comita LS, Queenborough SA, Murphy SJ, et al (2014) Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. J Ecol 102:845–856 . doi: 10.1111/1365-2745.12232

Corlett RT (2007) Pollination or seed dispersal: Which should we worry about most? In: Seed Dispersal: Theory and Its Application in a Changing World. pp 523–544

Cowan PE, Waddington DC (1990) Suppression of fruit production of the endemic forest tree, Elaeocarpus dentatus, by introduced marsupial brushtail possums, Trichosurus vulpecula. New Zeal J Bot 28:217–224 . doi: 10.1080/0028825X.1990.10412310

Daniel MJ (1973) Seasonal diet of the ship rat (Rattus R. rattus) in lowland forest in New Zealand. Proc New Zeal Ecol Soc 20:21–30

Doherty TS, Glen AS, Nimmo DG, et al (2016) Invasive predators and global biodiversity loss. Proc Natl Acad Sci 113:11261–11265 . doi: 10.1073/pnas.1602480113

Duncan RP, Boyer AG, Blackburn TM (2013) Magnitude and variation of prehistoric bird extinctions in the Pacific. Proc Natl Acad Sci 110:6436–6441 . doi: 10.1073/pnas.1216511110

Ellison AM (2004) Bayesian inference in ecology. Ecol Lett 7:509–520 . doi: 10.1111/j.1461-0248.2004.00603.x

Gibbs G (2010) Do New Zealand invertebrates reflect the dominance of birds in their evolutionary history? N. Z. J. Ecol. 34:152–157

Graham M, Veitch D, Aguilar G, Galbraith M (2013) Monitoring terrestrial bird populations on Tiritiri Matangi Island, Hauraki Gulf, New Zealand, 1987-2010. N Z J Ecol 37:359–369

Graham MF, Veitch CR (2002) Changes in bird numbers on Tiritiri Matangi Island, New Zealand, over the period of rat eradication. Turn Tide Erad Invasive Species Proc Int Conf Erad Isl Invasives 1971:414

Grant-Hoffman MN, Barboza PS (2010) Herbivory in invasive rats: Criteria for food selection. Biol Invasions 12:805–825 . doi: 10.1007/s10530-009-9503-7

Harper G (2006) Weka (Gallirallus australis) depredation of sooty shearwater/titi (Puffinus griseus) chicks. Notornis 53:318–320

Iles JM (2012) Is Maungatautari restoring bird pollination and seed dispersal services? University of Canterbury

Iles JM, Kelly D (2014) Restoring bird pollination of Fuchsia excorticata by mammalian predator control. N Z J Ecol 38:297–306

Innes J, Kelly D, Overton JMC, Gillies C (2010) Predation and other factors currently limiting New Zealand forest birds. N. Z. J. Ecol. 34:86–114

Kelly D, Geldenhuis A, James A, et al (2013) Of mast and mean: Differential-temperature cue makes mast seeding insensitive to climate change. Ecol Lett 16:90–98 . doi: 10.1111/ele.12020

Kelly D, Ladley JJ, Robertson AW, et al (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit- dispersal in New Zealand. N Z J Ecol 34:66–85

Kelly D, Sork VL (2002) Mast seeding in perennial plants: Why, how, where? Annu Rev Ecol Syst 33:427–447 . doi: 10.1146/annurev.ecolsys.33.020602.095433

King CM (2005) The Handbook of New Zealand Mammals (2nd ed.). Oxford University Press, Melbourne

Koenig WD, Kelly D, Sork VL, et al (2003) Dissecting components of population-level variation in seed production and the evolution of masting behavior. Oikos 102:581–591 . doi: 10.1034/j.1600-0706.2003.12272.x

Lee WG, Clout MN, Robertson HA, Bastow Wilson J (1991) Avian dispersers and fleshy fruits in New Zealand. Proc Int Orn Congr XX 1617–1623

Lettink. M, Hopkins G, Mayhew K (2010) Conservation status, threats and management options for the Open Bay Island skink (Oligosoma taumakae). New Zeal J Zool 37:225–234 . doi: 10.1080/03014223.2010.496488

Levine JM, Murrell DJ (2003) The community-level consequences of seed dispersal patterns. Annu Rev Ecol Evol Syst 34:549–574 . doi: 10.1146/annurev.ecolsys.34.011802.132400

Lord J (2002) Have frugivores influenced the evolution of fruit traits in New Zealand? In: DJ L, WR S, M G (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, WallingfoRd, UK, pp 55–68

McConkey KR, Prasad S, Corlett RT, et al (2012) Seed dispersal in changing landscapes. Biol. Conserv. 146:1–13

McNutt KL (1998) Impacts of reduced bird densities on pollination and dispersal mutualisms in New Zealand forests. Massey University, New Zealand

Meehan HJ, McConkey KR, Drake DR (2002) Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. J Biogeogr 29:695–712 . doi: 10.1046/j.1365-2699.2002.00718.x

Miskelly C, Beauchamp T (2004) Weka, a conservation dilemma. In: Restoring Kapiti: Nature's Second Chance. pp 81–88

Moles AT, Drake DR (1999) Post-dispersal seed predation on eleven large-seeded species from the New Zealand flora: A preliminary study in secondary forest. New Zeal J Bot 37:679–685 . doi: 10.1080/0028825X.1999.9512662doi.org/10.1080/0028825X.1999.9512662

Moorhouse RJ (1997) The diet of the North Island kaka (Nestor meridionalis septentrionalis) on Kapiti Island. N Z J Ecol 21:141–152 . doi: 10.2307/24054509

Morriss GA, Warburton B, Cross ML, Nugent G (2012) Hoarding behavior by ship rats (Rattus rattus) in captivity and its relevance to the effectiveness of pest control operations. Eur J Wildl Res 58:483–488 . doi: 10.1007/s10344-011-0562-6

Murphy DJ, Kelly D (2001) Scarce or distracted? Bellbird (Anthornis melanura) foraging and diet in an area of inadequate mistletoe pollination. N Z J Ecol 25:69–81

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol Evol 15 278-285 15:278–285 . doi: 10.1016/S0169-5347(00)01874-7

O'Connor SJ, Kelly D (2012) Seed dispersal of matai (Prumnopitys taxifolia) by feral pigs

(Sus scrofa). N Z J Ecol 36:

O'Farrill G, Galetti M, Campos-Arceiz A (2013) Frugivory and seed dispersal by tapirs: An insight on their ecological role. Integr. Zool. 8:4–17

Olson SL, James HF (1991) Descriptions of thirty-two new species of birds from the Hawaiian islands: part I. Non-passeriformes. Ornithol Monogr 1–88 . doi: 10.2307/40166794

Overdyck E, Clarkson BD, Laughlin DC, Gemmill CEC (2013) Testing broadcast seeding methods to restore urban forests in the presence of seed predators. Restor Ecol 21:763–769 . doi: 10.1111/j.1526-100X.2012.00933.x

Parkes JP, Byrom AE, Edge KA (2017) Eradicating mammals on New Zealand island reserves: What is left to do? N Z J Ecol 41: . doi: 10.20417/nzjecol.41.25

Pegman APMcK, Perry GLW, Clout MN (2017) Size-based fruit selection by a keystone avian frugivore and effects on seed viability. New Zeal J Bot 55:118–133 . doi: 10.1080/0028825X.2016.1247882

Pender RJ, Shiels AB, Bialic-Murphy L, Mosher SM (2013) Large-scale rodent control reduces pre- and post-dispersal seed predation of the endangered Hawaiian lobeliad, Cyanea superba subsp. superba (Campanulaceae). Biol Invasions 15:213–223 . doi: 10.1007/s10530-012-0280-3

R Development Core Team (2010) R: A language and environment for statistical computing. R Found Stat Comput Vienna, Austria

Robertson AW, Trass A, Ladley JJ, Kelly D (2006) Assessing the benefits of frugivory for seed germination: The importance of the deinhibition effect. Funct. Ecol. 20:58–66

Robertson C, Hyvőnen P, Fraser MJ, Pickard CR (2007) Atlas of Bird Distribution in New Zealand 1999-2004. Ornithological Society of New Zealand

Rogers HS, Buhle ER, HilleRisLambers J, et al (2017) Effects of an invasive predator cascade to plants via mutualism disruption. Nat Commun 8:14557 . doi: 10.1038/ncomms14557

Saunders A, Norton DA (2001) Ecological restoration at mainland islands in New Zealand. Biol Conserv 99:109–119 . doi: 10.1016/S0006-3207(00)00192-0

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: A conceptual review. New Phytol. 188:333–353

Sekercioglu CH, Daily GC, Ehrlich PR (2004) Ecosystem consequences of bird declines. Proc Natl Acad Sci 101:18042–18047 . doi: 10.1073/pnas.0408049101

Shiels AB, Drake DR (2015) Barriers to seed and seedling survival of once-common Hawaiian palms: The role of invasive rats and ungulates. AoB Plants 7:plv057 . doi: 10.1093/aobpla/plv057

Silberbauer RB (2013) Benefits of seed dispersal for escaping seed predation and examining the life history, host suitability/preference and impact of the polyphagous obligate seed predator Cryptaspasma querula. Massey University, New Zealand

Spiegelhalter DJ, Best NG, Carlin BP, Van Der Linde A (2002) Bayesian measures of model complexity and fit. J R Stat Soc Ser B Stat Methodol 64:583–616 . doi: 10.1111/1467-9868.00353

Starling-Windhof A, Massaro M, Briskie J V. (2011) Differential effects of exotic predator-control on nest success of native and introduced birds in New Zealand. Biol Invasions 13:1021–1028 . doi: 10.1007/s10530-010-9886-5

Steadman DW (1995) Prehistoric extinctions of Pacific Island birds: Biodiversity meets zooarchaeology. Science (80-) 267:1123–1131 . doi: 10.1126/science.267.5201.1123

Tanentzap AJ, Lloyd KM (2017) Fencing in nature? Predator exclusion restores habitat for native fauna and leads biodiversity to spill over into the wider landscape. Biol Conserv 214:119–126 . doi: 10.1016/j.biocon.2017.08.001

Tennyson AJD (2009) The origin and history of New Zealand's terrestrial vertebrates. N Z J Ecol 34:

Thomson C, Challies CN (1988) Diet of feral pigs in the podocarp-tawa forests of the Urewera Ranges. N. Z. J. Ecol. 11:73–78

Thorsen MJ, Seddon PJ, Dickinson KJM (2011) Faunal influences on New Zealand seed dispersal characteristics. Evol Ecol 25:1397–1426 . doi: 10.1007/s10682-011-9470-1

Towns DR (2009) Eradications as reverse invasions: Lessons from Pacific rat (rattus exulans) removals on New Zealand islands. Biol Invasions 11:1719–1733 . doi: 10.1007/s10530-008-9399-7

Towns DR, Atkinson IAE, Daugherty CH (2006) Have the harmful effects of introduced rats on islands been exaggerated? Biol Invasions 8:863–891 . doi: 10.1007/s10530-005-0421-z

Towns DR, Broome KG (2003) From small Maria to massive Campbell: Forty years of rat eradications from New Zealand islands. New Zeal J Zool 30:377–398 . doi: 10.1080/03014223.2003.9518348

Traveset A, Riera N (2005) Disruption of a plant-lizard seed dispersal system and its

ecological effects on a threatened endemic plant in the Balearic Islands. Conserv Biol 19:421–431 . doi: 10.1111/j.1523-1739.2005.00019.x

Vander Wall SB (1990) Food Hoarding in Animals. University of Chicago Press, Chicago

Wallace HM, Howell MG, Lee DJ (2008) Standard yet unusual mechanisms of long-distance dispersal: Seed dispersal of Corymbia torelliana by bees. Divers Distrib 14:87–94 . doi: 10.1111/j.1472-4642.2007.00427.x

Wandrag EM, Dunham AE, Duncan RP, Rogers HS (2017) Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings. Proc Natl Acad Sci 114:201709584 . doi: 10.1073/pnas.1709584114

Webb CJ, Kelly D (1993) The reproductive biology of the New Zealand flora. Trends Ecol. Evol. 8:442–447

Wenny DG (2002) Effects of human handling of seeds on seed removal by rodents. Am Midl Nat 147:404–408 . doi: 10.1674/0003-0031(2002)147[0404:EOHHOS]2.0.CO;2

Williams CK (1982) Nutritional properties of some fruits eaten by the possum Trichosurus vulpecular in a New Zealand boradleaf-podocarp forest. N Z J Ecol 5:16–20

Williams PA, Karl BJ, Bannister P, Lee WG (2000) Small mammals as potential seed dispersers in New Zealand. Austral Ecol 25:523–532 . doi: 10.1046/j.1442-9993.2000.01078.x

Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH (2008) Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. Proc Natl Acad Sci 105:7676–7680 . doi: 10.1073/pnas.0801507105

Wotton DM (2007) Consequences of dispersal failure: kereru and large seeds in New Zealand. University of Canterbury

Wotton DM, Drake DR, Powlesland RG, Ladley JJ (2016) The role of lizards as seed dispersers in New Zealand. J. R. Soc. New Zeal. 46:40–65

Wotton DM, Kelly D (2011) Frugivore loss limits recruitment of large-seeded trees. Proc R Soc B Biol Sci 278:3345–3354 . doi: 10.1098/rspb.2011.0185

Wright SJ, Zeballos H, Dominguez I, et al (2000) Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. Conserv Biol 14:227–239 . doi: 10.1046/j.1523-1739.2000.98333.x

Wyman TE (2013) Consequences of reduced bird densities for seed dispersal. University of Canterbury

Young LM, Kelly D, Nelson XJ (2012) Alpine flora may depend on declining frugivorous

parrot for seed dispersal. Biol Conserv 147:133–142 . doi:
10.1016/j.biocon.2011.12.023

UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

Deputy Vice-Chancellor's Office
Postgraduate Research Office

Co-Authorship Form

This form is to accompany the submission of any thesis that contains research reported in co-authored work that has been published, accepted for publication, or submitted for publication. A copy of this form should be included for each co-authored work that is included in the thesis. Completed forms should be included at the front (after the thesis abstract) of each copy of the thesis submitted for examination and library deposit.

Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter 5 – submitted to Austral Ecology

Carpenter JK, Kelly D. "Passive integrated transponder (PIT) tagged seeds reveal extremely long seed retention times in a flightless rail".

Please detail the nature and extent (%) of contribution by the candidate:

Jo Carpenter formulated research questions, designed the study, conducted fieldwork, analysed the data, created graphs, and wrote the manuscript (90%).

Certification by Co-authors:

If there is more than one co-author then a single co-author can sign on behalf of all

The undersigned certifies that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name: Dave Kelly Signature: Dave Kelly Date: *6/2/2019*

5

Passive integrated transponder (PIT) tagged seeds reveal extremely long seed retention times in a flightless rail (*Gallirallus australis*)

Unconsumed hīnau seed (left), and hīnau seed after 14 days inside a weka (right). Photo: Dave Kelly

5.1 Abstract

The length of time that animals retain seeds in their guts greatly influences the spatial pattern of seed dispersal. Flightless, omnivorous birds may have particularly long seed retention times that could accentuate their importance as seed dispersers. However, long retention times are usually measured by searching animal enclosures at intervals for defecated seeds, which can lead to data with considerable error and right-censored retention times. I used passive integrated transponder (PIT) tagged seeds to assess retention times in a flightless, omnivorous rail, the New Zealand weka (*Gallirallus australis*). I inserted PIT tags into miro (*Prumnopitys ferruginea*) and hīnau (*Elaeocarpus dentatus*) seeds and fed them to captive weka. PIT-tagged seeds were detected inside weka a mean of 10.6 times per day. Weka retained PIT-tagged miro seeds for a mean of 38.5 hours (1.6 days; range 1 – 379 hours) and a median of 8.2 hours. Hīnau seeds were retained for a mean of 125.2 hours (5.2 days; range 2.5 – 958 hours), and a median of 20.5 hours. These are some of the longest avian retention times ever recorded, and suggests that weka have the potential to disperse seeds very long distances, despite being flightless. PIT-tagged seeds offer excellent potential for measuring long retention times in other species.

5.1 Introduction

Seeds often depend on being eaten by frugivorous animals to escape from the (sometimes deadly; Bagchi et al. 2010) influence of their parents. The length of time that seeds remain in a disperser's gut (seed retention time) is very important, as it affects the probability of seeds being dispersed away from parent canopies. In addition, long seed retention times increase the likelihood of long distance dispersal events, which impact gene flow, metapopulation dynamics, range expansion rates, and colonization opportunities (Higgins and Richardson 1999; Cain et al. 2000; Nathan 2006).

The most-studied avian dispersers are volant, frugivorous species (Traveset 1998). However, the functional diversity provided by less obvious seed dispersers is increasingly recognised as an important driver of spatial patterns of seed dispersal (Calviño-Cancela 2002; Jordano et al. 2007; González-Varo et al. 2013). Flightless birds, while rarely included in seed dispersal studies, can be significant seed dispersers for several reasons (Bradford and Westcott 2010; Renison et al. 2010). Flightless birds may have longer seed retention times than volant birds as they do not need to quickly pass heavy seed 'ballast' in order to fly, and omnivory may further increase seed retention times (Afik and Karasov 1995; Yoshikawa et al. 2019). Longer seed retention times would increase the probability of long distance dispersal (e.g. Calviño-Cancela et al. 2006). However, there are few studies of seed retention times in flightless omnivorous birds.

While long seed retention times are important for seed dispersal, they are difficult to measure. Seed retention times are normally measured by feeding an animal fruits or artificial seed mimics (coloured buttons or beads) and subsequently searching its enclosure at intervals for droppings containing seeds or seed mimics (often once or twice a day; e.g. Willson 1989; Andriantsaralaza et al. 2014). Depending on how frequently searches take place, this method can result in considerable error in possible retention times. In addition, there is a significant risk that many seeds will not be discovered if enclosures are large and seeds are cryptic. Because typically not all seeds are recovered, it is difficult to be sure when the last seed has been voided by the

animal. While seed mimics are generally easier to find, they may have significantly different retention times due to them lacking traits of natural fruits (Traveset 1998).

Seeds containing a passive integrated transponder (PIT) tag offer a novel method of obtaining improved estimates of long seed retention times. A PIT tag is a glass-encapsulated microchip, measuring from 4 x 34 mm down to 1.5 x 7 mm, programmed with a unique alphanumeric code. A radio frequency identification (RFID) receiver-transmitter attached to an antenna reads the code remotely. Feeding an animal a PIT-tagged seed then regularly scanning the animal until the PIT-tagged seed is no longer detected could allow better estimates of long gut passage times without the need for continual observation or searches of enclosures for seeds. PIT-tagged seeds have previously been used to discover the location of seeds moved by scatter-hoarding rodents (Suselbeek et al. 2013), but have not to my knowledge been used in estimating seed retention times.

Here, I used PIT-tagged seeds to estimate the seed retention times of a flightless, omnivorous New Zealand rail, the weka (*Gallirallus australis*; Fig. 5.1b). Weka are one of New Zealand's largest extant endemic seed dispersers (mean weight 900 g, range 430 – 1700 g), and have recently been shown to be the most important disperser for some native tree species (Carpenter et al. 2018a). However, most seed dispersal research in New Zealand has focused on the kererū (*Hemiphaga novaeseelandiae* - an endemic pigeon), and other volant birds (Kelly et al. 2010), so data regarding the quality of seed dispersal provided by weka are still limited.

5.2 Methods

Weka occur across most habitat types in New Zealand (Beauchamp et al. 1999), although their abundance and range have decreased greatly since human arrival due to habitat loss, predation by exotic mammals, and drought-related starvation (Beauchamp et al. 1999; Robertson et al. 2007). Their diet is dominated by fruit and invertebrates but also includes lizards, carrion, and the eggs and chicks of ground nesting birds (Beauchamp et al. 1999). Weka consume the fruits of at least 26 native plant species, ranging in size from *Coprosma* spp. (4 mm diameter) to *Beilschmiedia*

tawa (15.5 mm)(Coleman et al. 1983; Beauchamp 1987; Clout and Hay 1989; Beauchamp et al. 1999). They swallow fruits whole and either defecate or regurgitate the seeds intact (Beauchamp 1987; Carpenter et al. 2018a).

I measured the seed retention times of weka for two relatively large-fruited plant species commonly eaten by weka. Miro (*Prumnopitys ferruginea*, Podocarpaceae) fruit are 12-15 mm in diameter (Kelly et al. 2010), with a pulpy exocarp and a hard, woody seed coat 1.5 – 2mm thick that encases the single seed. Hīnau (*Elaeocarpus dentatus*, Elaeocarpaceae) fruits average 9.2 mm diameter (maximum ~ 15 mm), with a carbohydrate-rich exocarp and mesocarp and a hard woody seed coat protecting the single seed (Kelly et al. 2010). Miro fruit were collected in May 2018 from Ulva Island (46° 92’ S, 168° 12’ E), and hīnau fruit were collected in June 2018 from the University of Canterbury campus (43° 52’ S, 172° 58’ E). I drilled a 13 x 2.5 mm hole into the long axis of each seed. I first removed the pulp from the miro seeds to prevent the seed slipping out of the vice while drilling. A single glass-encapsulated High Frequency PIT tag (12 x 2.15 mm, weight 0.1 g, Oregon RFID) was glued into the hole with epoxy resin (Fig. 5.1a). I did not weigh the seeds before and after modification, but as the seed material I removed was replaced by the PIT tag I feel that any differences are likely to be minor.

I conducted the gut passage trials with four captive weka (three females, and one male) held in two enclosures (250 m^2 and 110 m^2 in size) at Willowbank Wildlife Reserve (43° 46’ S, 172° 59’ E) in Christchurch. The enclosures included trees, shrubs, logs, a hill, and a pond. During the duration of the trial weka were kept on their regular diet of commercially available fruit and vegetables (apples, peas, etc.), commercial pet food, and seeds. Weka were fed at mid-morning each day. I offered the weka PIT-tagged seeds at various times of day, and recorded the time that each PIT-tagged seed was ingested. PIT-tagged seeds were smeared with cheese to make them more attractive to the birds. I used a Chafon 13.56MHz RFID ISO15693 middle range reader and a Chafon 13.56MHz ABS handheld high frequency antenna (352 x 332 x 22 mm) to detect PIT-tagged seeds inside the weka. The square antenna was fixed to the door of the weka’s food shelter, so weka walked through the antenna frequently to reach their food (Fig. 5.1c). A laptop attached to the reader logged the identity and time when PIT-

tagged seeds were detected by the scanner. This system allowed the simultaneous reading of multiple PIT tags, which is important when birds have multiple seeds in their gut. All experimental protocols were approved by the University of Canterbury Animal Ethics Committee (Application 2017-22R), and conducted in accordance with relevant guidelines.

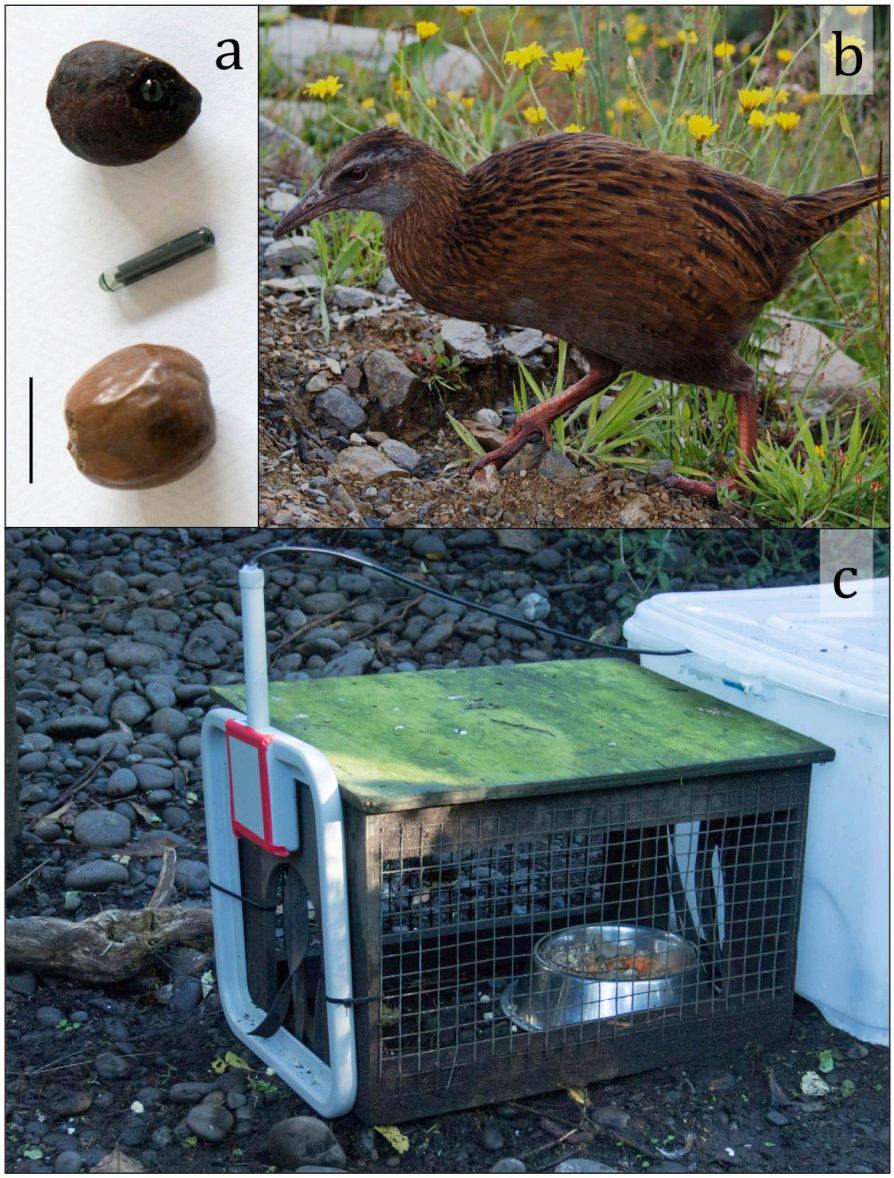


Figure 5.1. *A) From top to bottom: Miro (Prumnopitys ferruginea) seed with PIT tag inserted inside before epoxy resin was applied; 12.5 mm long PIT tag; hīnau (Elaeocarpus dentatus) seed with PIT tag inserted inside. Scale bar is 10 mm. B) Weka. C) Photo showing the antenna (grey) attached to the weka food shelter. Weka had to move through the antenna to access their food. The antenna is attached to an RFID scanner and laptop inside the white box.*

I calculated the time that elapsed between each PIT-tagged seed being eaten and the last time it was detected by the scanner. Since each tag was scanned ~10 times per day, including overnight, this minimum gut passage time will not greatly underestimate the exact time to defecation. When an individual had multiple PIT-tagged seeds in its gut, I also calculated the detection success rate for each seed while it was known to be in the bird by calculating what proportion of scans of the bird (based on any of its ingested seeds being detected) also detected the target seed. The distribution of seed retention times for the two plant species was not normal or log-normal, so I used a Kruskall-Wallis test to see whether seed retention times differed between the two plant species. I did not have sufficient data to test for variation among individual birds, so data from all individuals was pooled for the Kruskall-Wallis test.

After the trials ended I searched one of the enclosures for the seeds that had experienced the longest retention times to check whether they were intact. As seeds were extremely difficult to find visually (due to the substrate in the enclosure) I used the RFID antenna (attached to the scanner and laptop) to scan the ground, working in a sweeping motion.

5.3 Results

The four weka consumed 19 PIT-tagged miro seeds and 21 PIT-tagged hīnau seeds, with each bird consuming between 4 and 15 seeds. Three of the birds consumed seeds from both species. The PIT-tagged seeds were easily detected inside the birds' guts by the scanner antenna, with each PIT-tagged seed being detected an average of 10.6 times per day. As PIT tag detectability is affected by the angle that the PIT tag is on and whether birds went all the way through the antenna, not all PIT-tagged seeds were detected every time the birds passed through the scanner antenna. However, each PIT-tagged seed was detected 79.7% of the time on average. PIT-tagged seeds were detected at all hours of the day except for between midnight and 5am, where birds were presumably sleeping and were therefore unlikely to defecate anyhow (Appendix 5.5.1). I visually examined the distribution of times that PIT-tagged seeds were detected for each individual and found little individual variation, with all individuals

having the same distribution (i.e., all individuals entered the food shelter at all hours of the day except for between midnight and 5am). Therefore, the seed retention times I estimated based on the last detection time are likely to be only small underestimates. I recorded weka consuming some PIT-tagged seeds that were never subsequently detected by the scanner, but this was rare (1 out of 19 seeds for miro, and 3 out of 21 hīnau seeds). In these cases, I believe the bird regurgitated the seeds before passing through the scanner. I therefore used the first scan where other seeds were detected since feeding the missing seeds as an indicator of their retention time.

The weka had very long seed retention times (Fig. 5.2). The mean seed retention time for miro was 38.5 hours (SD = 85), with a range of 1 – 379 hours (approximately 15 days) and a median of 8.2 hours. The mean retention time for hīnau was 125.2 hours (SD = 252.2), with a range of 2.5 – 958 hours (approximately 40 days) and a median of 20.5 hours. Hīnau seed retention times did not differ from miro seed retention times (Kruskall-Wallis test, $\chi^2 = 2.6$, df = 1, p = 0.10).

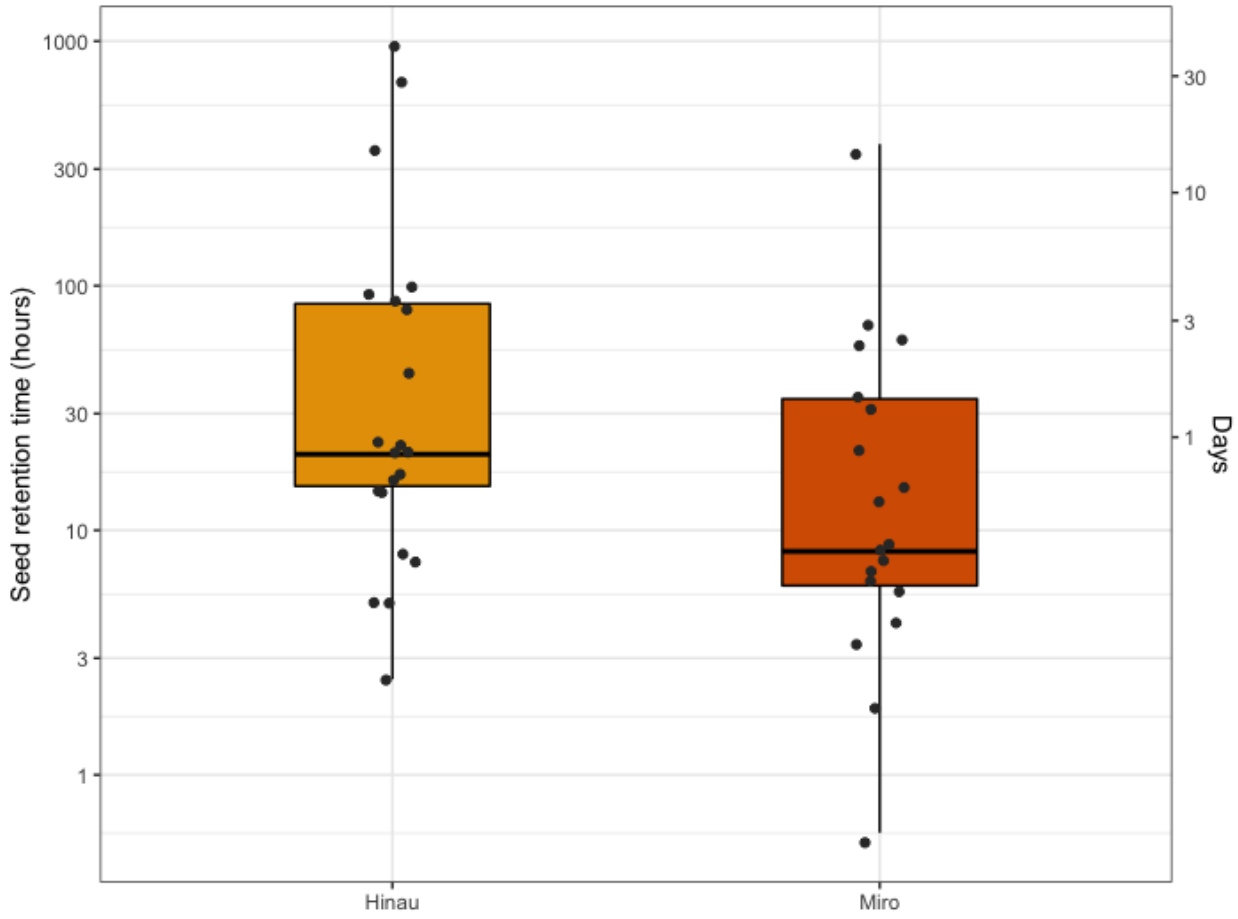


Figure 5.2. *Boxplot showing distribution of weka gut retention times (log scale) for seeds of hīnau (Elaeocarpus dentatus, n = 21) and miro (Prumnopitys ferruginea, n = 19). The grey dots show the actual data points, while the boxplot shows median, interquartile range, and minimum and maximum.*

Two weeks after the trials finished, I relocated 7 seeds from the largest enclosure using the antenna and scanner, including the two seeds that had been inside the weka for 14 and 15 days. The scanner detected a further 8 seeds buried in the ground which I did not examine. All of the seeds were intact, but some were buried up to 10 cm deep and were still very difficult to isolate even when the scanner indicated their locations.

5.4 Discussion

5.4.1 Using PIT tags to estimate seed retention times

PIT-tagged seeds offered an efficient method of estimating seed retention times in weka, avoiding the difficulties associated with searching enclosures for highly cryptic seeds repeatedly over more than 6 weeks. In addition, the ability to use the antenna and scanner to locate a subsample of passed seeds to check their condition is a real strength of the method. PIT-tagged seeds could be an effective way of assessing long seed retention times in other species, although some limitations exist. I recommend that the animals are observed until their first scan occurs, to avoid the risk of missing seeds if there is an unusually short seed retention time. In addition, the seeds used must be large enough to hold a PIT tag, and have a hard seed coat that can be drilled into without losing structural integrity. Animals must also be small enough to pass through an antenna. Some antennas come shaped as wands, which could be passed over the animal to detect PIT-tagged seeds, but I have not tested how well wand antennae would detect seeds inside an animal. However, waterfowl, small mammals, and tortoises could all be ideal candidates for estimating long seed retention times using PIT-tagged seeds with pass-through antennae.

5.4.2 Seed retention times in weka

The PIT-tagged seeds showed that weka, a flightless omnivorous rail, have the longest avian seed retention times yet recorded. The times are much longer than seed retention times for both flightless bird species such as southern cassowaries (*Casuarius casuarius*), and volant species such as the kererū (Fig. 5.3). While longer gut passage times have been recorded for a few species using dyes or synthetic particle markers (e.g. Fritz et al. 2012), those results are not directly comparable as they can give very different results to seed retention times. To my knowledge, emus (*Dromaius novaehollandiae*), least sandpipers (*Calidris minutilla*), and killdeers (*Charadrius vociferus*) are the only avian species with comparable reported seed retention times to weka (Proctor 1968; Calviño-Cancela et al. 2006). The only quantitative study on emu seed retention times using actual seeds (rather than seed mimics) found that ~90% of

seeds were recovered within 24 hours, with a maximum retention time of 264 hours (Calviño-Cancela et al. 2008), which are nearly as long as weka. Killdeers and least sandpipers had maximum seed retention times of 340 and 216 hours, respectively (Proctor 1968), but mean seed retention times were not reported. In comparison, most volant passerines have seed retention times of less than 60 minutes (Sorensen 1984; Clench and Mathias 1992; Murphy et al. 1993).

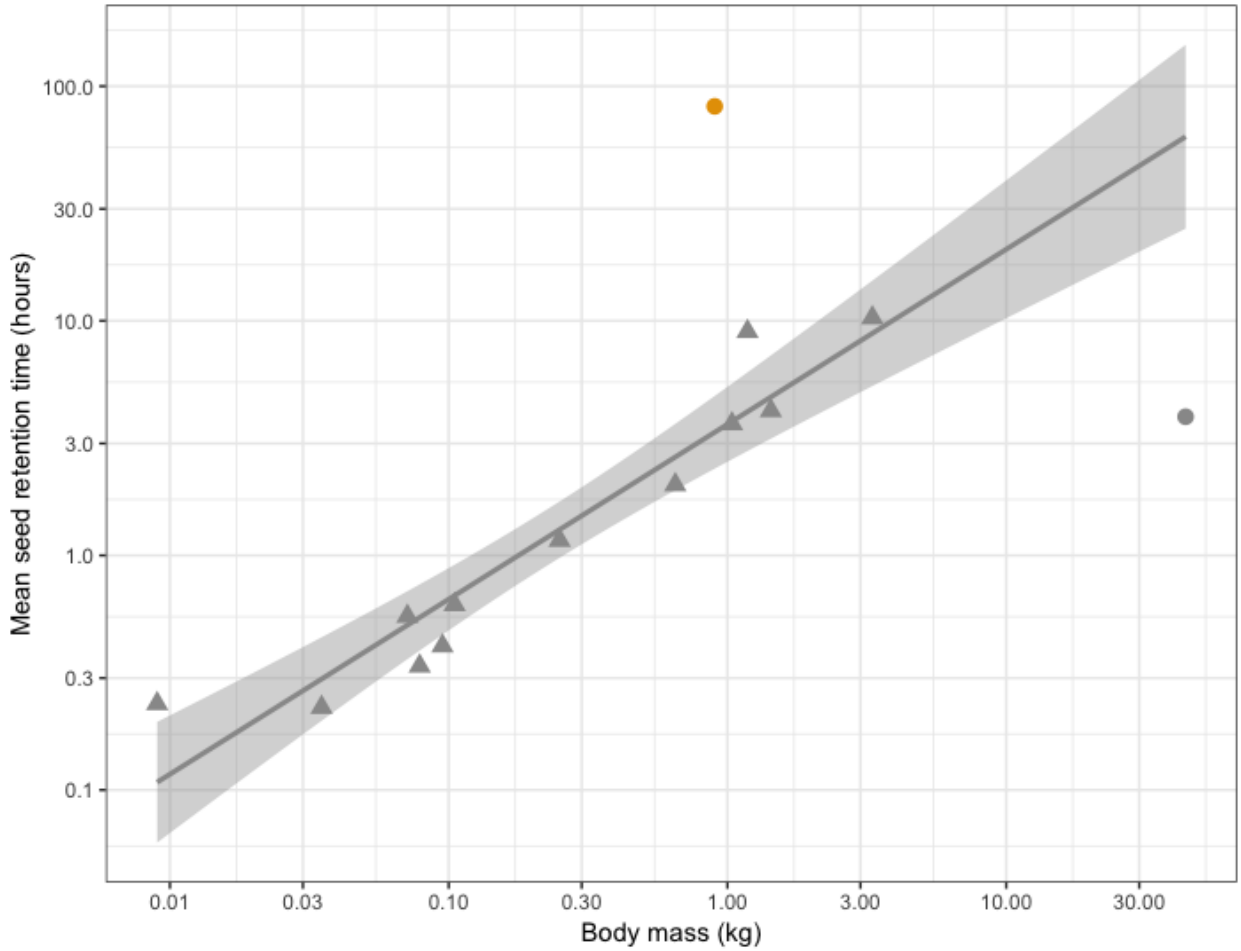


Figure 5.3. *Log mean seed retention time (averaged across all plant species when more than one was measured) vs. log bird body mass for weka (orange circle), the flightless Southern cassowary (Casuarius casuarius) (black circle), and 12 volant bird species (black triangles). From right to left on the graph the volant species are greylag goose (Anser anser), black-casqued hornbill (Ceratogymna atrata), mallard (Anas platyrhynchos), brown-cheeked hornbill (C. cylindricus), kererū (Hemiphaga novaeseelandiae), rwenzori turaco (Musophaga johnstoni), tūī (Prosthemadera novaeseelandiae), Eurasian blackbird (Turdus merula), brown-eared bulbul (Hypsipetes amaurotis), common starling (Sturnus vulgaris), hihi (Notiomystis cincta), and mistletoebird (Dicaeum hirundinaceum). Linear regression line fitted to volant birds with 95% confidence intervals to show the relationship between mass and seed*

retention time. Graph modified from Wotton and Kelly (2011) using data from (Sorensen 1984; Karasov and Levey 1990; Murphy et al. 1993; Sun et al. 1997; Trass 2000; Holbrook and Smith 2000; Fukui 2003; Westcott et al. 2005; O'Connor 2006; Wotton et al. 2008; García-Álvarez et al. 2015).

The long seed retention times of weka are probably due to their relatively large size, flightlessness, and diet. There is a positive relationship between bird size and seed retention times (Herrera 1984; Wotton and Kelly 2012; Yoshikawa et al. 2019). Flightlessness probably further lengthens seed retention times as flightless birds have no evolutionary selection for short intestines that quickly remove heavy seed 'ballast' in order to fly (as volant birds do; Caviedes-Vidal et al. 2007), and can thus afford to retain gut contents for longer for more complete digestion. Consequently, flightless birds should therefore have both longer intestines and seed retention times than their volant counterparts. Diet and digestive strategy are also strong predictors of seed retention time in birds, with specialist frugivores having shorter seed retention times than herbivores or omnivores (Yoshikawa et al. 2019). Weka may have slow gut passage in order to effectively process invertebrates, animal proteins, and coarse vegetable matter (Afik and Karasov 1995; Karasov et al. 2011). This probably goes some way to explaining why weka have longer seed retention times than flightless cassowaries - which are specialist frugivores - even though cassowaries are so much larger than weka (weka 1 kg, cassowary 50-76 kg). However, it is still puzzling that weka seed retention times are longer than that for emus (40 kg), when emus have a herbivorous diet that should necessitate longer gut passage times than omnivory because of the fermentation required.

Seed retention times are also affected by seed size and fruit traits (Traveset 1998; Pollux et al. 2006, 2007). Smaller seeds than those that I tested may have shorter retention times, although the relationship between seed size and retention time is inconsistent among avian dispersers (Wotton et al. 2008; Chang et al. 2012). The secondary metabolites within fruit pulp can also decrease or increase seed retention times (Murray et al. 1994; Tewksbury et al. 2008; Baldwin and Whitehead 2015). Here I found long retention times both in hīnau (which had the fruit pulp intact) and miro

(which had the fruit pulp removed), although I cannot determine what might have happened if fruit pulp had been removed for hīnau or left intact for miro.

Interestingly, weka retain grit and small stones in their gizzard to help process food, and seems likely that the four seeds which remained inside the weka for >14 days were acting as substitute gizzard stones. Five of New Zealand's tree species, including miro and hīnau, have unusually thick, woody seed coats which have previously been identified as "anachronistic", or maladapted for dispersal by the contemporary fauna (Kelly et al. 2010). My finding that weka retain some of these seeds for longer than two weeks offers a possible explanation for these species' unusually thick seed coats (relative to other New Zealand trees). Consistent with this hypothesis, the recovered seeds which spent two weeks in the gut had polished seed coats but appeared otherwise undamaged.

Long seed retention times can have trade-offs between increased seed dispersal distances and decreased germination of seeds (Charalambidou et al. 2003). Assessing the germination success of my weka-passed seeds was not possible as inserting PIT tags damages the seeds, but anecdotal evidence suggests that seeds germinate well after weka gut passage, with seed-filled weka droppings being used to germinate seedlings for plant nurseries (Geoff Davidson pers. comm.). Carpenter et al. (2018b) also demonstrated that mild abrasion improved the germination of hīnau seeds, so the mild abrasion that occurs when seeds pass through the grit-filled gizzard of weka could be beneficial for certain plant species.

I acknowledge several limitations of my study, that are inherent in most seed retention studies performed to date (Oleksy et al. 2017). First, birds were on a captive diet which could alter seed retention times compared to birds eating only wild food, although the macronutrient ratios of the captive diet compared to wild diet are probably similar. In addition, I did not measure how much each bird consumed each day, which could have influenced individual variation in seed retention times. Lastly, it is also possible that the cheese I smeared onto the fruits to make them more attractive to the weka may have altered seed retention times.

The long seed retention times I observed in weka will have important flow-on effects for the proportion of seeds that weka disperse away from parent canopies, and the probability of long distance dispersal events. While weka generally maintain year-round home ranges that can range in size from 1.25 to 743 hectares (Bramley and Veltman 2000; Watts 2013), they also have remarkable mobility and dispersal capabilities, and have been recorded moving distances as large as 300 kilometres over a six-week period (Robertson 1976; Coleman et al. 1983). These movements coupled with their long seed retention times could make them significant long distance seed dispersers under certain circumstances. Information on the seed dispersal capabilities of weka is important, because in New Zealand weka are commonly excluded from restoration projects due to their predatory impacts on other native fauna (Miskelly and Beauchamp 2004), and have also been lost from large tracts of their native range (Beauchamp et al. 1999). More widely, Steadman (2006) estimates that almost every Pacific island had one or more endemic flightless rails, but nearly all (an estimated 450 to 1600 species) went extinct after human colonization in the last 3000 years. Given the importance of weka for seed dispersal in New Zealand, those Pacific island extinctions may have had large and widespread impacts on seed dispersal across one-third of the Earth's surface.

5.5 Appendices

5.5.1 Bird scan times

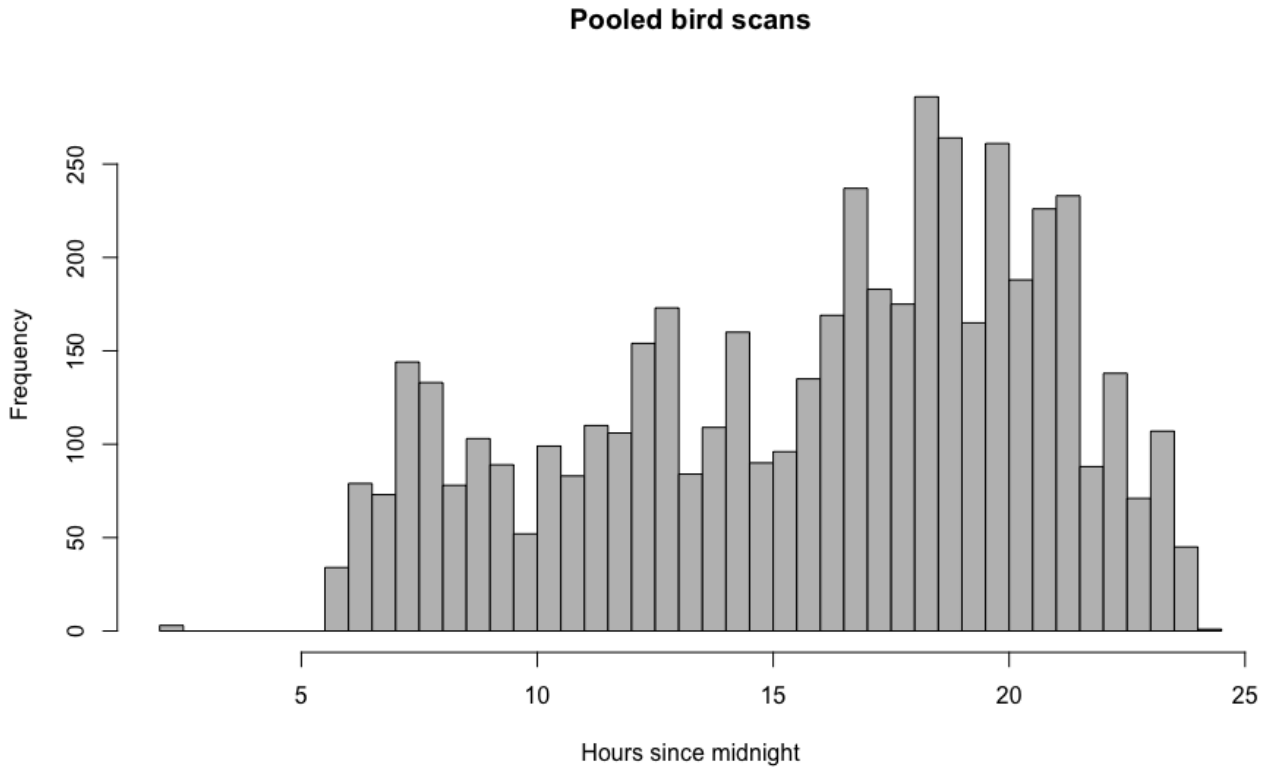


Figure showing time of day when PIT-tagged seeds were detected. Detections occurred at all hours of the day except for between midnight and 5am, when birds were presumed to be sleeping. Data are pooled from all four individual weka as visual examinations of the distribution for each bird indicated that they were very similar.

5.6 References

Afik D, Karasov WH (1995) The trade-offs between digestion rate and efficiency in warblers and their ecological implications. Ecology 76:2247–2257 . doi: 10.2307/1941699

Andriantsaralaza S, Pedrono M, Tassin J, et al (2014) The role of extinct giant tortoises in the germination of extant baobab Adansonia rubrostipa seeds in Madagascar. Afr J Ecol 52:246–249 . doi: 10.1111/aje.12101

Bagchi R, Swinfield T, Gallery RE, et al (2010) Testing the Janzen-Connell mechanism: Pathogens cause overcompensating density dependence in a tropical tree. Ecol Lett 13:1262–1269 . doi: 10.1111/j.1461-0248.2010.01520.x

Baldwin JW, Whitehead SR (2015) Fruit secondary compounds mediate the retention time of seeds in the guts of Neotropical fruit bats. Oecologia 177:453–466 . doi: 10.1007/s00442-014-3096-2

Beauchamp A (1987) A population study of the weka, Gallirallus australis, on Kapiti Island. Victoria University of Wellington

Beauchamp AJ, Butler DJ, King D (1999) Weka (Gallirallus australis) recovery plan 1999-2009. Threatened Species Recovery Plan 29.

Bradford MG, Westcott DA (2010) Consequences of southern cassowary (Casuarius casuarius, L.) gut passage and deposition pattern on the germination of rainforest seeds. Austral Ecol 35:325–333 . doi: 10.1111/j.1442-9993.2009.02041.x

Bramley GN, Veltman CJ (2000) Directions for future management of North Island Weka Gallirallus australis greyi to improve survival and productivity in situ. Bird Conserv Int 10:241–253 . doi: 10.1017/S0959270900000204

Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations. Am J Bot 87:1217–1227 . doi: 10.2307/2656714

Calviño-Cancela AM, Dunn RR, Etten EJB Van, et al (2006) Emus as non-standard seed dispersers and their potential for long-distance dispersal. Ecography (Cop) 29:632–640

Calviño-Cancela M (2002) Spatial patterns of seed dispersal and seedling recruitment in Corema album (Empetraceae): The importance of unspecialized dispersers for regeneration. J Ecol 90:775–784 . doi: 10.1046/j.1365-2745.2002.00711.x

Calviño-Cancela M, He T, Lamont BB (2008) Distribution of myrmecochorous species over the landscape and their potential long-distance dispersal by emus and kangaroos.

Divers Distrib 14:11–17 . doi: 10.1111/j.1472-4642.2007.00402.x

Carpenter JK, Kelly D, Moltchanova E, O'Donnell CFJ (2018a) Introduction of mammalian seed predators and the loss of an endemic flightless bird impair seed dispersal of the New Zealand tree Elaeocarpus dentatus. Ecol. Evol. 1–13

Carpenter JK, Wood JR, Wilmshurst JM, Kelly D (2018b) An avian seed dispersal paradox: New zealand's extinct megafaunal birds did not disperse large seeds. Proc R Soc B Biol Sci 285: . doi: 10.1098/rspb.2018.0352

Caviedes-Vidal E, McWhorter TJ, Lavin SR, et al (2007) The digestive adaptation of flying vertebrates: High intestinal paracellular absorption compensates for smaller guts. Proc Natl Acad Sci United States Am 104:19132–19137 . doi: 10.1073/pnas.0703159104

Chang S-Y, Lee Y-F, Kuo Y-M, Chen J-H (2012) Frugivory by Taiwan Barbets (Megalaima nuchalis) and the effects of deinhibition and scarification on seed germination. Can J Zool 90:640–650 . doi: 10.1139/z2012-030

Charalambidou I, Santamaria L, Langevoord O (2003) Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of Ruppia maritima seeds. Funct Ecol 17:747–753 . doi: 10.1111/j.1365-2435.2003.00787.x

Clench MH, Mathias JR (1992) Intestinal transit: How can it be delayed long enough for birds to act as long-distance dispersal agents? Auk 109:933–936

Clout MN, Hay JR (1989) The importance of birds As browsers, pollinators and seed dispersers in New Zealand forests. N Z J Ecol 27–33 . doi: 10.2307/24053245

Coleman JD, Warburton B, Green WQ (1983) Some population statistics and movements of the Western Weka. Notornis 30:93–107

Fritz J, Hammer S, Hebel C, et al (2012) Retention of solutes and different-sized particles in the digestive tract of the ostrich (Struthio camelus massaicus), and a comparison with mammals and reptiles. Comp Biochem Physiol - A Mol Integr Physiol 163:56–65 . doi: 10.1016/j.cbpa.2012.05.184

Fukui A (2003) Relationship between seed retention time in bird's gut and fruit characteristics. Ornithol Sci 2:41–48 . doi: 10.2326/osj.2.41

García-Álvarez A, van Leeuwen CHA, Luque CJ, et al (2015) Internal transport of alien and native plants by geese and ducks: An experimental study. Freshw Biol 60:1316–1329 . doi: 10.1111/fwb.12567

González-Varo JP, López-Bao J V., Guitián J (2013) Functional diversity among seed

dispersal kernels generated by carnivorous mammals. J Anim Ecol 82:562–571 . doi: 10.1111/1365-2656.12024

Herrera CM (1984) Adaptation to frugivory of Mediterranean avian seed dispersers. Ecology 65:609–617 . doi: 10.2307/1941423

Higgins SI, Richardson DM (1999) Predicting plant migration rates in a changing world: The eole of long-distance dispersal. Am Nat 153:464–475 . doi: 10.1086/303193

Holbrook KM, Smith TB (2000) Seed dispersal and movement patterns in two species of Ceratogymna hornbills in a West African tropical lowland forest. Oecologia 125:249–257 . doi: 10.1007/s004420000445

Jordano P, Garcia C, Godoy JA, Garcia-Castano JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. Proc Natl Acad Sci 104:3278–3282 . doi: 10.1073/pnas.0606793104

Karasov W, Levey D (1990) Digestive system trade-offs and adaptations of frugivorous passerine birds. Physiol Zool 63:1248–1270 . doi: 10.1086/physzool.63.6.30152643

Karasov WH, Martínez del Rio C, Caviedes-Vidal E (2011) Ecological physiology of diet and digestive systems. Annu Rev Physiol 73:69–93 . doi: 10.1146/annurev-physiol-012110-142152

Kelly D, Ladley JJ, Robertson AW, et al (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit- dispersal in New Zealand. N Z J Ecol 34:66–85

Miskelly C, Beauchamp T (2004) Weka, a conservation dilemma. In: Restoring Kapiti: Nature's Second Chance. pp 81–88

Murphy SR, Reid N, Yan Z, Venables WN (1993) Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers: effects on seedling establishment. Oecologia 93:171–176 . doi: 10.1007/BF00317667

Murray KG, Russell S, Picone CM, et al (1994) Fruit laxatives and seed passage rates in frugivores: Consequences for plant reproductive success. Ecology 75:989–994

Nathan R (2006) Long-distance dispersal of plants. Science (80-.). 313:786–788

O'Connor S-J (2006) Modelling seed dispersal by tūī. University of Canterbury

Oleksy R, Giuggioli L, McKetterick TJ, et al (2017) Flying foxes create extensive seed shadows and enhance germination success of pioneer plant species in deforested Madagascan landscapes. PLoS One 12:e0184023 . doi: 10.1371/journal.pone.0184023

Pollux BJA, De Jong M, Steegh A, et al (2006) The effect of seed morphology on the

potential dispersal of aquatic macrophytes by the common carp (Cyprinus carpio). Freshw Biol 51:2063–2071 . doi: 10.1111/j.1365-2427.2006.01637.x

Pollux BJA, Ouborg NJ, Van Groenendael JM, Klaassen M (2007) Consequences of intraspecific seed-size variation in Sparganium emersum for dispersal by fish. Funct Ecol 21:1084–1091 . doi: 10.1111/j.1365-2435.2007.01313.x

Proctor VW (1968) Long-distance dispersal of seeds by retention in digestive tract of birds. Science (80-) 160:321–322 . doi: 10.1126/science.160.3825.321

Renison D, Valladares G, Martella MB (2010) The effect of passage through the gut of the Greater Rhea (Rhea americana) on germination of tree seeds: Implications for forest restoration. Emu 110:125–131 . doi: 10.1071/MU09090

Robertson C, Hyvőnen P, Fraser MJ, Pickard CR (2007) Atlas of Bird Distribution in New Zealand 1999-2004. Ornithological Society of New Zealand

Robertson DB (1976) Weka liberation in Northland. Notornis 23:213–219

Sorensen AE (1984) Nutrition, energy and passage time: Experiments with fruit preference in European Blackbirds (Turdus merula). J Anim Ecol 53:545–557 . doi: 10.2307/4533

Steadman DW (2006) Extinction and biogeography of tropical Pacific birds. University of Chicago Press, Chicago

Sun C, Ives AR, Kraeuter HJ, Moermond TC (1997) Effectiveness of three turacos as seed dispersers in a tropical montane forest. Oecologia 112:94–103 . doi: 10.1007/s004420050288

Suselbeek L, Jansen PA, Prins HHT, Steele MA (2013) Tracking rodent-dispersed large seeds with Passive Integrated Transponder (PIT) tags. Methods Ecol Evol 4:513–519 . doi: 10.1111/2041-210X.12027

Tewksbury JJ, Levey DJ, Huizinga M, et al (2008) Costs and benefits of capsaicin-mediated control of gut retention in dispersers of wild chilies. Ecology 89:107–117 . doi: 10.1890/07-0445.1

Trass AP (2000) Invasion of woody species into weed infested areas. Massey University

Traveset A (1998) Effect of seed passage through vertebrate frugivores' guts on germination: A review. Perspect Plant Ecol Evol Syst 1:151–190 . doi: 10.1078/1433-8319-00057

Watts J (2013) Reintroducing Buff Weka (Gallirallus australis hectori) to an Unfenced Mainland Island. University of Otago

Westcott DA, Bentrupperbäumer J, Bradford MG, McKeown A (2005) Incorporating

patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. Oecologia 146:57–67 . doi: 10.1007/s00442-005-0178-1

Willson MF (1989) Gut retention times of experimental pseudoseeds by emus. Biotropica 21:210–213 . doi: 10.2307/2388645

Wotton DM, Clout MN, Kelly D (2008) Seed retention times in the New Zealand pigeon (Hemiphaga novaezeelandiae novaeseelandiae). N Z J Ecol 32:1–6

Wotton DM, Kelly D (2012) Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. J Biogeogr 39:1973–1983 . doi: 10.1111/jbi.12000

Wotton DM, Kelly D (2011) Frugivore loss limits recruitment of large-seeded trees. Proc R Soc B Biol Sci 278:3345–3354 . doi: 10.1098/rspb.2011.0185

Yoshikawa T, Kawakami K, Masaki T (2019) Allometric scaling of seed retention time in seed dispersers and its application to estimation of seed dispersal potentials of theropod dinosaurs. Oikos. doi: 10.1111/oik.05827

UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

Deputy Vice-Chancellor's Office
Postgraduate Research Office

Co-Authorship Form

This form is to accompany the submission of any thesis that contains research reported in co-authored work that has been published, accepted for publication, or submitted for publication. A copy of this form should be included for each co-authored work that is included in the thesis. Completed forms should be included at the front (after the thesis abstract) of each copy of the thesis submitted for examination and library deposit.

Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter 6 – submitted to Royal Society Open Science

Carpenter JK, O'Donnell CF, Moltchanova E, Kelly D. "Long seed dispersal distances by an inquisitive flightless rail are reduced by interaction with humans".

Please detail the nature and extent (%) of contribution by the candidate:

Jo Carpenter formulated research questions, designed the study, conducted fieldwork, analysed the data (but did not write the code for the mechanistic model), created graphs, and wrote the manuscript (80%).

Certification by Co-authors:

If there is more than one co-author then a single co-author can sign on behalf of all

The undersigned certifies that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name: Dave Kelly Signature: Dave Kelly Date: *6/2/2019*

6

Long seed dispersal distances by a flightless rail (*Gallirallus australis*) are reduced by interaction with humans

Weka congregating at Goldsborough Reserve campsite.

6.1 Abstract

Animals in modified habitats typically have reduced movement patterns, with worrying ramifications for ecosystem functions such as seed dispersal. Human presence is becoming increasingly ubiquitous even in landscapes that appear unaffected by structural modifications, but the influence this has on the vagility and effectiveness of seed dispersing animals is unknown. The New Zealand weka (*Gallirallus australis*) is an inquisitive flightless rail that frequently congregates in areas of high human use. Weka are important seed dispersers in New Zealand, yet the quality of seed dispersal they provide is still poorly understood. I estimated seed dispersal distances of weka for two plant species (*Prumnopitys ferruginea* and *Elaeocarpus dentatus*) and tested how human interaction affected these dispersal distances. I estimated weka seed dispersal distances by combining GPS data from 39 weka over three sites with weka seed retention time data in a mechanistic model. Weka were highly effective dispersers, dispersing 93-96% of seeds away from parent canopies, and 1% of seeds over 1 kilometre. Mean dispersal distances for *P. ferruginea* and *E. dentatus* were 125.5 m and 142.8 m, respectively. However, weka that occupied areas of high human use (i.e. campsites, n = 10) within two of the sites had 34.8-40.9% shorter seed dispersal distances than their more remote counterparts (n = 11). This represents an example of cryptic function loss, where although weka are still present in the ecosystem their seed dispersal services are impaired by human interaction. More broadly, the effectiveness of weka as seed dispersers demonstrates that omnivorous flightless rails can perform high quality seed dispersal services. The mass extinction of >450 rail species across the Pacific may therefore represent a widespread yet overlooked loss of dispersal function.

6.2 Introduction

Humans have modified approximately 50 to 70% of the earth's surface (Barnosky et al. 2012), with profound consequences for the species that use those habitats. Landscape modification consists of structural changes such as roads or deforestation, and non-structural changes such as noise pollution or frequent human activity (McConkey and O'Farrill 2016). Unsurprisingly, animals in these anthropogenically disturbed habitats move and behave differently to their undisturbed counterparts. Most studies report decreased vagility of animals living in modified habitats, driven by both negative effects such as barriers to movement (e.g. Sawyer et al. 2013), and positive effects such as enhanced resources at modified sites (e.g. crops, supplementary feeding, and water sources) that mean animals have to travel less to meet their resource requirements (e.g. Jones et al. 2014). Due to these mechanisms, movements of mammals in intensively human-modified areas are reduced by half to two-thirds compared with individuals in areas with less human modification (Tucker et al. 2018), and similar reductions in vagility have been documented for other taxa (e.g. Laurance et al. 2004; Brehme et al. 2013).

Reduced animal movements could affect important ecosystem functions such as seed dispersal. The movement patterns of seed dispersing animals have large effects on how far seeds travel, the individual survival prospects of seeds, and the probability of long-distance dispersal events (Howe and Smallwood 1982). Seed deposition patterns then affect recruitment and colonization rates, the ability of plants to escape climate change effects, gene flow between plant populations, and forest community composition (Nathan and Muller-Landau 2000; Levine and Murrell 2003; Godinez-Alvarez et al. 2009; Jordano et al. 2011; Wandrag et al. 2017). All these problems are magnified because at the same time as fragmentation reduces the mobility of seed dispersers, it increases the dispersal distances required to maintain gene flow and may reduce the density of dispersers. In fragmented landscapes, maintaining gene flow between patches of remaining habitat requires longer dispersal distances, but reduced vagility of dispersers makes that less likely (Uriarte et al. 2011). For example, carnivorous mammals moved seeds shorter distances in fragmented forests compared

to more intact habitats (Herrera et al. 2016), potentially resulting in reduced gene flow between forest fragments. In addition, many seed disperser guilds in modified habitats have greatly declined in both abundance and species diversity, so the maintenance of seed dispersal services may rely on a fraction of the species that it once did (Bregman et al. 2014; Morante-Filho et al. 2015). Therefore, anthropogenic landscapes may induce cascading effects for plant communities by truncating the movements of seed dispersers.

Even in landscapes that do not suffer from structural anthropogenic modifications like roads or habitat fragmentation, human presence is becoming increasingly pervasive, and this may directly affect the vagility and effectiveness of seed dispersing animals. For example, mantled howler monkeys (*Alouatta palliata mexicana*) inhabiting a forest fragment used for nature-based tourism spent more time in lower quality habitat when the number of human visitors increased (Aguilar-Melo et al. 2013). Similarly, rhesus macaques have shortened daily ranges when they are fed by people, suggesting reduced seed dispersal distances (Sengupta et al. 2015). However, very few studies have investigated how human presence may alter the movement and effectiveness of seed dispersing animals, despite the fact that even "wild" landscapes are becoming increasingly crowded with people.

In New Zealand, one species that has a high level of human interaction is the weka (*Gallirallus australis*), an inquisitive flightless rail. Weka are bold, opportunistic birds that frequently aggregate at areas of high human use, such as campsites or picnic areas (Miskelly and Beauchamp 2004). Their charisma and cunning results in them often being fed by, and stealing food from, people (Miskelly and Beauchamp 2004). Recently weka have been shown to be important seed dispersers for some New Zealand plant species (Carpenter et al. 2018), but they have been studied much less than volant, frugivorous birds such as the kererū (New Zealand wood pigeon *Hemiphaga novaeseelandiae*; Kelly et al. 2010). Weka have the potential to move seeds long distances as they have some of the longest avian seed retention times in the world (mean 1.6-5.2 days, maximum 40 days: Chapter 5). However, no one has measured how far weka typically disperse seeds. In addition, understanding the quality of seed dispersal provided by weka may give insights into the seed dispersal

capabilities of flightless rails as a group, which were once common across the Pacific but have suffered widespread extinctions there in the last 3000 years (Steadman 2006).

I used a mechanistic model approach to study weka seed dispersal. Mechanistic models combine data on seed retention times and high-resolution animal movement patterns to estimate the magnitude and frequency of potential seed dispersal distances (Nathan et al. 2003). My aims were to: 1) estimate weka seed dispersal distances for two large-seeded plant species; and 2) investigate how interaction with humans affects weka seed dispersal distances. I predicted that weka that spent a lot of time in areas of high human use would move less far, and therefore disperse seeds shorter distances, than their counterparts in more remote areas.

6.3 Methods

6.3.1 Study species and sites

Weka are one of the largest (mean 900 g, range 400-1700 g) extant seed dispersing birds in New Zealand (Robertson and Heather 1999). They occur across most habitat types, although their abundance and range have decreased alarmingly since human arrival due to habitat loss, predation by exotic mammals, and drought-related starvation (Beauchamp et al. 1999). Their wild diet is dominated by fruit and invertebrates but also includes lizards, carrion, and the eggs and chicks of ground nesting birds (Beauchamp et al. 1999). They swallow fruits whole and either defecate or regurgitate the seeds intact (Beauchamp 1987; Carpenter et al. 2018).

I modelled seed dispersal distances for two large-seeded plant species commonly eaten by weka – miro (*Prumnopitys ferruginea,* Podocarpaceae) and hīnau (*Elaeocarpus dentatus,* Elaeocarpaceae). Miro is a tree that grows to 25 m tall and occurs throughout New Zealand. Its fruits are 12-15 mm in diameter, with a fleshy exocarp and a hard, woody seedcoat 1.5-2 mm thick that encases the single seed. Hīnau trees grow up to 20 m tall and occur in lowland conifer-broadleaf forest throughout the North Island and the northern South Island. Its fruits average 9.2 mm

diameter, with a carbohydrate-rich exocarp and mesocarp and a hard woody seedcoat protecting the single seed.

I used three sites to collect high-resolution movement data for weka in order to estimate weka seed dispersal distances. Lake Mahinapua Scenic Reserve (42°79'25 S, 170°90'53 E) and Goldsborough Reserve (42°67'55 S, 171°12'42 E) are two areas of dense podocarp-broadleaved forest near Hokitika on the West Coast of the South Island. The third site, Ulva Island (46°93'18 S, 168°12'53 E), is a 267 ha island off Rakiura/Stewart Island, which is free of exotic mammalian predators (e.g. rats *Rattus* spp.), and covered in podocarp-broadleaf forest.

At two of these sites I could also assess how human presence affects weka seed dispersal distances. Lake Mahinapua and Goldsborough both contain popular Department of Conservation campsites, which are areas of high human use. These campsites are surrounded by dense podocarp-broadleaf forest, which is rarely entered by people. This allowed us to sample weka that contact humans frequently (those that spent time in the campsite) versus infrequently (those in the forest away from the campsite). Ulva Island had no hub of high human use so was not used for this analysis, but was still used to estimate overall weka seed dispersal distances.

6.3.2 Collection of GPS data

Collection of movement data occurred between February and May 2018 (the peak of the fruiting season for most bird dispersed New Zealand plant species; Moore and Edgar 1970). I captured 46 weka using either a ground noose (Watts 2013) or hand net, and took weight and bill measurements from each individual. Where possible, I sexed and aged (juvenile or adult) each bird based on its weight, bill measurements, wing spurs, and vocalisations (Beauchamp 1998). I used electrical heatshrink plastic to combine into one package an igot-u120 GPS logger and a Sirtrack Ultimate Lite single-stage VHF transmitter (combined weight 30 g), and secured it to the bird using a backpack harness. Birds were only fitted with a GPS and harness if the combined unit was no more than 5% of their body weight. GPS tags were programmed to attempt a fix every 15 minutes. After 14 days, I recaptured the weka and removed the transmitter and harness. Following difficulties recapturing some of the Lake

Mahinapua birds, I fitted birds from Goldsborough and Ulva Island with a harness that included a degradable weaklink (Karl and Clout 1987). Three weka were unable to be recaptured after the two week monitoring period, and four weka had their GPS devices fail. This left me with GPS data from 39 weka (Lake Mahinapua n = 13, Goldsborough n = 12, Ulva Island n = 14), including both sexes and juvenile and adult individuals.

I excluded from analysis all GPS fixes that were obtained using fewer than 4 satellites due to concerns about their lack of accuracy (Morris and Conner 2017). I also visually inspected the waypoints for each bird and removed any waypoints that appeared incorrect (i.e., waypoints that occurred so far away from the last recoded waypoint that the bird could not have moved there in that time, and single waypoints that occurred large distances away from the bird's usual home range with no waypoints in between). Previous studies have shown that the GPS tags I used have a mean location error of <10 m, even under dense cover (Morris and Conner 2017).

6.3.3 Mechanistic model

I developed a mechanistic seed dispersal model using the GPS data from all three sites and weka seed retention times to estimate the distribution of weka dispersal distances (dispersal kernels) for miro and hīnau (see Appendices 6.6.1 for r code for model). Seed retention times were simulated by randomly sampling 100,000 seed retention times from empirical weka seed retention time data for the two plant species (Chapter 5). I removed two of the hīnau seed retention datapoints (30 and 40 days) as they were longer than the 14 day GPS logs. That means that my estimated dispersal distances were biased towards shorter seed retention times.

Weka can forage at all times of the day and night (Beauchamp 1987, Carpenter 2017 unpubl. data), so I simulated ingestion for all hours of the day. The model simulated ingestion of each seed at randomly selected times during the bird's tracking log. As GPS waypoints were only obtained at 15 minute intervals, the model frequently sampled times that did not have a specific waypoint attached to them. When this occurred, the model interpolated the location of the bird (drew a line between the last recorded waypoint and the next recorded waypoint and calculated the location of the bird between those two fixes, assuming that the bird was moving in a linear direction

at a constant speed). The model then used the randomly sampled seed retention time to determine the time of defecation, found the location of the bird at that time, and measured the distance between the ingestion location and defecation location. The process was repeated to obtain a probability distribution of dispersal distances for each bird, which were then pooled to obtain the mean dispersal distance for each plant species.

When the simulated seed retention time ran past the end of the tracking session, the resulting dispersal distance was recorded as missing. This means that dispersal distances were further biased towards shorter seed retention times. For miro an average of 5% of dispersal distances were missing (range 0-20% for different birds) because the track stopped before the seed emerged, and for hīnau an average of 4.25% dispersal distances were missing (range 0-31%).

6.3.4 Statistical analysis

In order to identify the birds that had a high level of human interaction (Lake Mahinapua and Goldsborough birds only), I used bivariate normal kernel functions to estimate the utilization distribution of each bird's home range (Worton 1989). Individuals whose core home range (defined as the 70% isopleth; Watts 2013) overlapped with the campground were defined as birds that had a high level of human interaction (hereafter referred to as 'camp followers', n = 10). Birds at the two sites whose core home range did not overlap with a campground were categorised as 'remote' birds (n = 11). I only used adult birds for the analysis as juvenile weka have different movement patterns to adult birds (Bramley and Veltman 2000) and all the juvenile birds I captured were camp followers, which would have confounded the model. I used a linear mixed effects model to assess whether camp followers had shorter mean dispersal distances than remote birds. Median dispersal distance for each bird for each plant species (as obtained from the mechanistic model) was the response variable, while human interaction (or not) and plant species were the fixed effects (with an interaction term). I used the median dispersal distance for each bird because I was interested in variability between individuals rather than within individuals. I log-transformed the median dispersal distance for each bird to improve

normality. I used Levene's tests to confirm homogeneity of variances. Sex was initially included in the model as a fixed effect but it was nonsignificant so I removed it. Site and bird ID were included as random effects. All analyses were conducted in R version 3.5.1, using the packages lme4, lmerTest, adehabitatHR, and car.

6.4 Results

6.4.1 Weka seed dispersal kernels

The mechanistic model estimated that weka dispersed 93-96% of seeds away from the parent tree, with <7% of the seeds being dispersed beneath the parent (assuming a canopy radius of 10 m; Table 6.1). Just over half of the seeds were dispersed within 100 m of the source, but approximately 40% of seeds were also dispersed over 100 m, with around 1% of seeds being dispersed over 1 km. The dispersal kernels appeared to have a leptokurtic distribution for both plant species (Fig. 6.1). Miro and hīnau mean dispersal distances were broadly similar (Table 6.1).

Table 6.1. *Weka seed dispersal distances (m) and distribution patterns (% vs distance) generated from the mechanistic model for miro (Prumnopitys ferruginea) and hīnau (Elaeocarpus dentatus).*

	Dispersal distance (m)		**Seeds dispersed (%)**			
Plant species	Mean (± 1 SD)	Maximum	<10 m	10-100 m	100-1000 m	>1000 m
Miro	125.5 (± 175.3)	2,332.9	7	54	38.2	0.8
Hīnau	142.8 (± 197.9)	2,112.7	4	52	42.9	1.1

Table 6.2. *Outputs of linear mixed effects model of dispersal distances conducted by weka with high human interaction (camp followers) and low human interaction (remote birds) for miro (Prumnopitys ferruginea) and hīnau (Elaeocarpus dentatus. Human interaction is a significant fixed effect*.

Random effects	**Variance**	**Std. Dev.**
Site	0.09	0.31
Individual	0.2	0.44

Fixed effects	**Estimate**	**Std. Error**	**t value**	***p* value**
(Intercept)	4.31	0.26	16.57	0.013*
Not human habituated	0.48	0.2	2.43	0.025*
Plant species	-0.1	0.4	-2.41	0.026*
Not human habituated*plant species	-0.07	0.06	-1.19	0.249

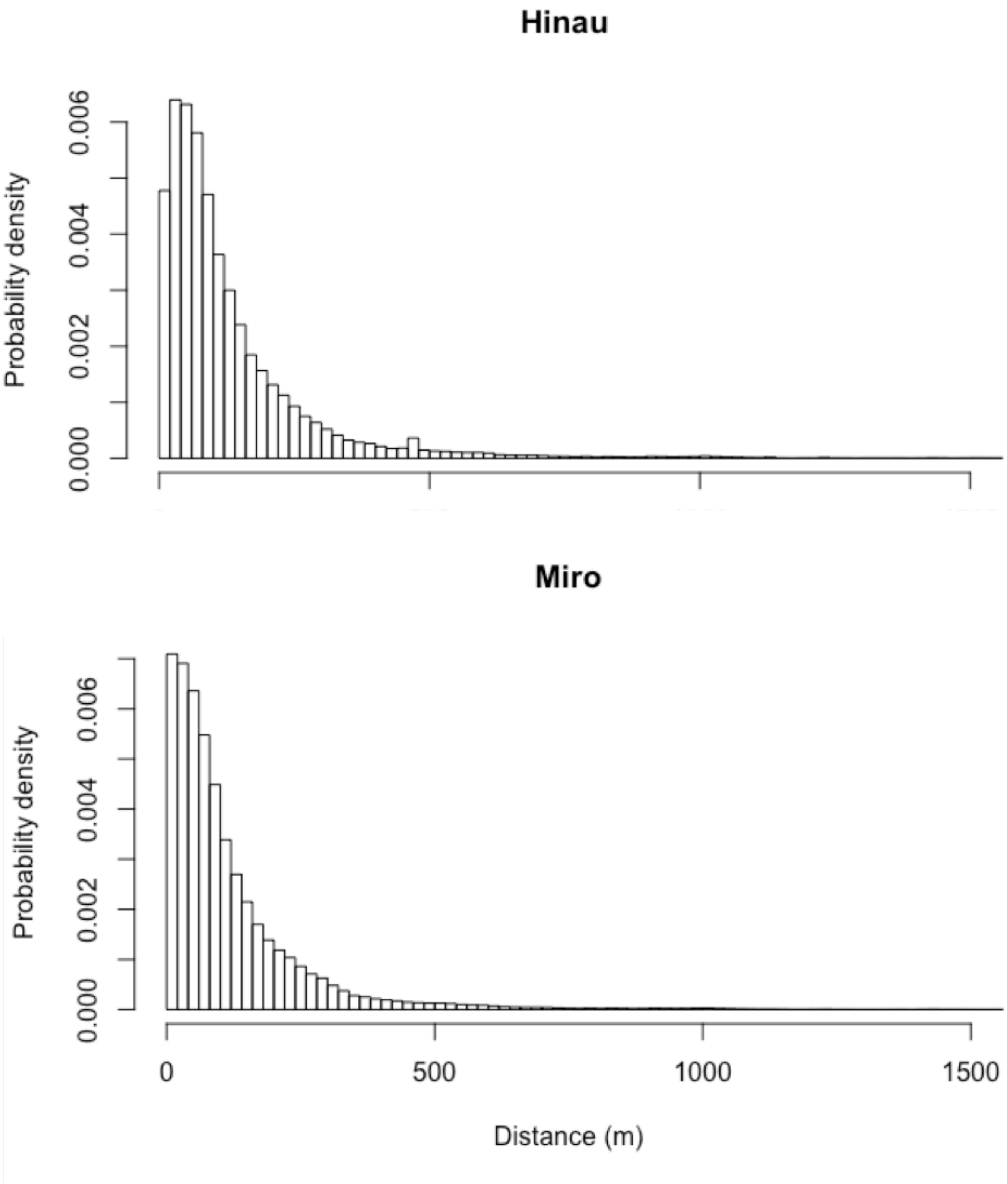


Figure 6.1. *Estimated probability distributions of weka (Gallirallus australis) seed dispersal distances at 20 m intervals for miro (Prumnopitys ferruginea) and hīnau (Elaeocarpus dentatus). Dispersal distances were generated using a mechanistic model that incorporated empirical data for individual weka movements and seed retention times.*

6.4.2 The effect of human interaction on the mean dispersal distances by weka

The linear mixed effect model demonstrated that camp follower weka dispersed hīnau and miro seeds significantly shorter distances than remote birds (Table 6.2). I estimated the mean dispersal distances for camp followers and remote birds (using the median dispersal distance for each individual bird) and found that miro seeds were

dispersed 53.4% further by remote birds (mean ± SE miro dispersal distance = 113.5 ± 20.2 m) compared to camp followers (74 ± 11.5 m) (Figure 6.2). Hīnau seeds were dispersed 69.3% further by remote birds (mean + SE hīnau dispersal distance = 138.8 ± 27.4 m) compared to camp followers (81.9 ± 12.7 m) (Figure 6.2).

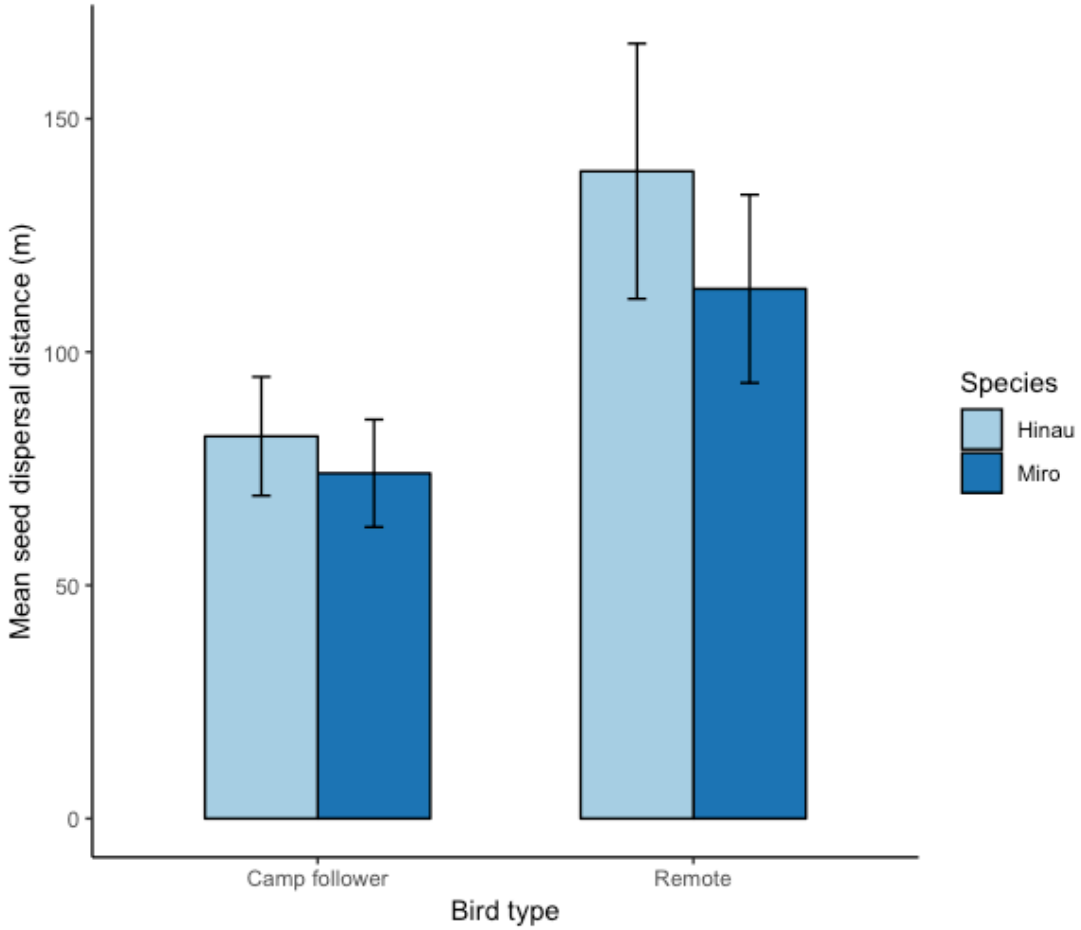


Figure 6.2. *Mean dispersal distances for hīnau (Elaeocarpus dentatus) and miro (Prumnopitys ferruginea) for "camp follower" weka (Gallirallus australis) that experienced a lot of human interaction (n = 10), and "remote" weka that had very little human interaction (n = 11). Linear mixed effects models showed the differences were significant for both species; see Table 6.2.*

6.5 Discussion

6.5.1 Weka seed dispersal kernels

Weka dispersal kernels appeared to be leptokurtic in shape, with just over half the seeds being deposited within 100 m of the source tree, followed by a rapid decline and a long tail out beyond 1000 m. This distribution is typical for animal mediated seed dispersal kernels (Nathan et al. 2008). However, because dispersal distances were large relative to canopy area, remarkably few seeds (4-7%) were deposited by weka beneath parent canopies. Since seeds that are deposited beneath parent canopies can suffer from disproportionate mortality due to density- and distant-dependent mortality (Comita et al. 2014), this result demonstrates that weka perform highly effective seed dispersal. As a comparison, the kererū, New Zealand's largest volant seed disperser, is relatively sedentary and disperses 13 - 34% of seeds beneath parent canopies (Wotton and Kelly 2012), so weka provide higher quality seed dispersal than kererū in this respect.

Despite being flightless, the mean dispersal distances of weka compare favourably to dispersal distances calculated for some of New Zealand's volant frugivores. Weka dispersal distances are greater than those calculated for kererū using a similar mechanistic model (61-98 m; Wotton and Kelly 2012). They are probably also greater than bellbird (*Anthornis melanura*) dispersal distances, given bellbird's small home range size (0.02 ha: Anderson and Craig 2003), but this still remains to be tested. However, weka seed dispersal distances are smaller than those estimated for tūī (*Prosthemadera novaeseelandiae*), a highly mobile passerine (214-231 m; O'Connor 2006), although the maximum dispersal distances calculated for tūī (2.2 km) are similar to weka. These results suggest that weka contribute non-redundantly to seed dispersal kernels by providing a complementary service to other New Zealand frugivores.

While weka seed dispersal distances are probably constrained by their home range sizes, their extremely long seed retention times (up to 40 days: Carpenter 2018 unpubl. data) mean that they have considerable potential to occasionally move seeds very long distances. As I only recorded weka movements for 14 days I had a limited capacity for

recording any rare long distance movements, although some juvenile weka moved over 1-2 kilometres away from their usual range. Interestingly, some adult weka on Ulva Island also moved 1-2 kilometres away from their usual home ranges, perhaps to take advantage of resources on beaches. Although flightless, weka are proficient swimmers and easily cross environmental barriers such as major rivers, lakes, and mountain ranges (Coleman et al. 1983). Coleman et al. (1983) recorded an adult male weka moving 35 kilometres away from their study site, with one juvenile moving 9 kilometres away, and translocated weka have been recorded moving 600 kilometres over a 6 week period. These occasional long distance movements, coupled with seed retention times that can reach 40 days, demonstrate that weka almost certainly generate rare very long distance dispersal events beyond what could be documented with my mechanistic model (which also underestimated dispersal distances for several technical reasons as noted in Methods). These long distance dispersal events could have quite a profound influence on enhancing genetic flow across extensive landscape scales.

6.5.2 The influence of humans on weka seed dispersal distances

I found that weka that spent a large amount of time at places of high human use dispersed hīnau and miro seeds significantly shorter distances than their more remote counterparts. The differences in dispersal distances between camp followers and remote birds were large, with remote birds dispersing seeds 53-69% further than camp followers. Reduced dispersal distances could easily influence the likelihood of seeds reaching suitable microsites. For example, in fragmented habitats a truncation of seed dispersal distances could be enough to reduce the number of seeds dispersed to suitable habitat fragments, thereby reducing gene flow between plant populations.

While I did not investigate the mechanisms driving this pattern in weka, provisioning by humans probably plays a large role in shortening the seed dispersal distances of camp follower birds. Weka that scavenge calorie-rich food at campsites or are deliberately fed by people (a common sight at campsites and picnic areas) would have to move less far to meet their energy requirements than birds that solely eat a wild diet. Several other studies have found that animals move less when they are

provisioned. Supplementary feeding decreased the home range size of red deer (*Cervus elaphus*) in Slovenia (Jerina 2012), and anthropogenic food resources led to smaller home ranges of raccoons (*Procyon lotor*) in Illinois, USA (Prange et al. 2004). Provisioning by humans is also likely to lead to decreased levels of frugivory in weka, although I did not measure whether human-habituated weka consumed less wild fruit. Similarly, Sengupta et al. (2015) demonstrated that provisioned rhesus macaques had decreased frugivory and seed dispersal activities.

My results provide an example of how the increasing ubiquity of people across the globe may have hidden consequences for seed dispersal processes, although the impacts of human presence on seed disperser behaviour will differ depending on the mechanisms involved. This finding is an example of cryptic function loss – where the ecological function of an animal population is significantly altered as a result of anthropogenic disturbance, even though the species is still present in the ecosystem (McConkey and O'Farrill 2016) and in fact is paradoxically increased in visibility by the same processes that simultaneously decrease its effectiveness for dispersal services.

6.5.3 Conservation implications in New Zealand and elsewhere

Weka are important, yet unappreciated, seed dispersers in New Zealand (Carpenter et al. 2018). They have been recorded consuming the fruits of over 26 native plant species, including some of New Zealand's largest-seeded species (Clout and Hay 1989), and the fruits of low-growing divaricating shrubs. My study has shown that weka also provide highly effective seed dispersal services, by dispersing 93-96% of seeds away from parent canopies – a higher proportion than kererū , which is often said to be New Zealand's most important seed disperser (discussed in Kelly et al. 2010). In addition, weka contribute to gene flow between plant populations by dispersing a reasonable proportion of seeds beyond one kilometre. Unfortunately, weka are controversial for New Zealand conservation managers because of the predatory impacts they have on other native fauna. This has led to them being frequently excluded from restoration projects (Miskelly and Beauchamp 2004), even though they have been lost from large areas of their native range, and are still threatened by exotic mammalian predators. I urge conservation managers to consider the positive contributions weka can also make

to ecosystem functioning when debating their presence in restoration projects. In addition, greater attempts should be made to discourage people from feeding weka. Not only is provisioning weka with human food probably not very healthy for the birds themselves, it also may impair their effectiveness as seed dispersers.

More broadly, my research into the seed dispersal capabilities of weka suggests that other rails across the Pacific may have been important seed dispersers, even though they are rarely mentioned as such. Steadman (2006) estimates at least 450 rail species have gone extinct across the Pacific in the last 3000 years, and the ecological consequences of those losses are still unknown. Even if just a small fraction of those species had the seed dispersal capabilities of weka, then the loss of Pacific rails may represent one of the most widespread yet least appreciated losses of dispersal function ever recorded.

6.6 Appendices

6.6.1 Code for mechanistic model

```
# 28/05/2018 updated 08/06/2018
#Updated more by Jo on 14/09/2018 (stopped using Gamma dist and
 used actual seed retention times instead)
# by Elena Moltchanova

rm(list=ls())
#library(geosphere)
load("~/Desktop/waypoints.Rdata")

# auxiliarly: sampling from truncated gamma
rtgamma <-
 function(n,a,b,upper=Inf){qgamma(runif(n)*pgamma(upper,a,b),a,b
 )}

# auxiliarly: haversine
hav <- function(theta){(1-cos(theta))/2}

# waypoints contain the information on individual birds: time
 and location
Nbirds <- length(waypoints)

# number of waypoints for each bird, maxtime (length of
 observation) for each bird
maxtime <- nwpts <- numeric(Nbirds)
minlat <- maxlat <- minlon <- maxlon <- numeric(Nbirds)
for(i in 1:Nbirds){
 nwpts[i] <- dim(waypoints[[i]])[1]
 maxtime[i] <- max(waypoints[[i]]$time)
 minlat[i] <-  min(waypoints[[i]]$Latitude)
 maxlat[i] <-  min(waypoints[[i]]$Latitude)
 minlon[i] <-  min(waypoints[[i]]$Longitude)
 maxlon[i] <-  min(waypoints[[i]]$Longitude)
}

# idea: sample a random vector of Nseeds seed retention times
# guttime measured in HOURS

set.seed(20180528)
Nseed <- 10^5

# estimating the distances travelled by the seed
```

```
dist.est <- array(dim=c(Nbirds,Nseed))

# start of bird-loop

for(bird in 1:Nbirds){print(bird)
# gut time for hinau
  my.guttime.list<-c(355.51, 7.43, 7.43, 47.06, 20.46, 21,
 20.46, 20.46, 103.15, 103.15, 15.16, 15.30, 15.30, 15.46,
 84.45, 84.45, 2.46, 5.45, 5.45)
# I do not like truncation, let's talk censoring
  guttime <- sample(my.guttime.list,size=Nseed,replace=T)
# random time of ingestion
guttime0 <- runif(Nseed,0,maxtime[bird]-guttime)
# time of exit
guttime1 <- guttime0 + guttime

# so we randomly choose guttime and randomly place it anywhere
 within the birds trajectory

# if it fits
guttime.ok <- (!is.na(guttime0)); n.ok <- sum(guttime.ok)

# interval during which the ingestion happens
interval0 <- apply(
(array(guttime0[guttime.ok],dim=c(n.ok,nwpts[bird]-1))>=
 t(array(waypoints[[bird]]$time[-nwpts[bird]],dim=c(nwpts[bird]-
 1,n.ok))))&
(array(guttime0[guttime.ok],dim=c(n.ok,nwpts[bird]-1))<
 t(array(waypoints[[bird]]$time[-1],dim=c(nwpts[bird]-
 1,n.ok)))),1,which)

### so... what are the coordinates at the beginning and end of
 the interval?
t00 <- waypoints[[bird]]$time[interval0]
lat00 <- waypoints[[bird]]$Latitude[interval0]
lon00 <- waypoints[[bird]]$Longitude[interval0]
t01 <- waypoints[[bird]]$time[interval0+1]
lat01 <- waypoints[[bird]]$Latitude[interval0+1]
lon01 <- waypoints[[bird]]$Longitude[interval0+1]

# so the actual coordinates are
lat0 <- lat00+(lat01-lat00)/(t01-t00)*(guttime0[guttime.ok]-t00)
lon0 <- lon00+(lon01-lon00)/(t01-t00)*(guttime0[guttime.ok]-t00)

# interval during which the exit happens
interval1 <- apply(
(array(guttime1[guttime.ok],dim=c(n.ok,nwpts[bird]-1))>=
```

```
 t(array(waypoints[[bird]]$time[-nwpts[bird]],dim=c(nwpts[bird]-
 1,n.ok))))&
(array(guttime1[guttime.ok],dim=c(n.ok,nwpts[bird]-1))<
 t(array(waypoints[[bird]]$time[-1],dim=c(nwpts[bird]-
 1,n.ok)))),1,which)

### so... what are the coordinates at the beginning and end of
 the interval?
t00 <- waypoints[[bird]]$time[interval1]
lat00 <- waypoints[[bird]]$Latitude[interval1]
lon00 <- waypoints[[bird]]$Longitude[interval1]
t01 <- waypoints[[bird]]$time[interval1+1]
lat01 <- waypoints[[bird]]$Latitude[interval1+1]
lon01 <- waypoints[[bird]]$Longitude[interval1+1]

# so the actual coordinates are
lat1 <- lat00+(lat01-lat00)/(t01-t00)*(guttime1[guttime.ok]-t00)
lon1 <- lon00+(lon01-lon00)/(t01-t00)*(guttime1[guttime.ok]-t00)

# distances (m) between two sets of coordinates

h.tmp <- hav((lat1-
 lat0)*pi/180)+cos(lat1*pi/180)*cos(lat0*pi/180)*hav((lon1-
 lon0)*pi/180)
dist.est[bird,1:n.ok] <- 2*6378137*asin(sqrt(h.tmp))
} # end of bird-loop

### PLOTTING THE RESULTS
xcol <- terrain.colors(Nbirds)
plot(density(dist.est[1,],bw=25),ylim=c(0,.02),xlim=c(0,quantile
 (c(dist.est),.99)),col=xcol[1],
 main='',sub='')
for(i in 2:Nbirds){lines(density(dist.est[i,]),col=xcol[i])}
lines(density(c(dist.est),bw=25),lwd=3)
warnings()
# proportion of censored:
apply(is.na(dist.est),1,mean)

save(dist.est, file="~/Desktop/hinaudists.Rdata")
```

6.7 References

Aguilar-Melo AR, Andresen E, Cristóbal-Azkarate J, et al (2013) Behavioral and physiological responses to subgroup size and number of people in howler monkeys inhabiting a forest fragment used for nature-based tourism. Am J Primatol 75:1108–1116 . doi: 10.1002/ajp.22172

Anderson SH, Craig JL (2003) Breeding biology of bellbirds (Anthornis melanura) on Tiritiri Matangi Island. Notornis 50:75–82

Barnosky AD, Hadly EA, Bascompte J, et al (2012) Approaching a state shift in Earth's biosphere. Nature 486:52–58 . doi: 10.1038/nature11018

Beauchamp A (1987) A population study of the weka, Gallirallus australis, on Kapiti Island. Victoria University of Wellington

Beauchamp AJ (1998) The ageing of Weka (Gallirallus australis) using measurements, soft parts, plumage and wing spurs. Notornis 45:167–176

Beauchamp AJ, Butler DJ, King D (1999) Weka (Gallirallus australis) recovery plan 1999-2009. Threatened Species Recovery Plan 29.

Bramley GN, Veltman CJ (2000) Directions for future management of North Island Weka Gallirallus australis greyi to improve survival and productivity in situ. Bird Conserv Int

10:241–253 . doi: 10.1017/S0959270900000204

Bregman TP, Sekercioglu CH, Tobias JA (2014) Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. Biol Conserv 169:372–383 . doi: 10.1016/j.biocon.2013.11.024

Brehme CS, Tracey JA, Mcclenaghan LR, Fisher RN (2013) Permeability of roads to movement of scrubland lizards and small mammals. Conserv Biol 27:710–720 . doi: 10.1111/cobi.12081

Carpenter JK, Kelly D, Moltchanova E, O'Donnell CFJ (2018) Introduction of mammalian seed predators and the loss of an endemic flightless bird impair seed dispersal of the New Zealand tree Elaeocarpus dentatus. Ecol. Evol. 1–13

Clout MN, Hay JR (1989) The importance of birds As browsers, pollinators and seed dispersers in New Zealand forests. N Z J Ecol 27–33 . doi: 10.2307/24053245

Coleman JD, Warburton B, Green WQ (1983) Some population statistics and movements of the Western Weka. Notornis 30:93–107

Comita LS, Queenborough SA, Murphy SJ, et al (2014) Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. J Ecol 102:845–856 . doi: 10.1111/1365-2745.12232

Godinez-Alvarez AH, Valiente-banuet A, Rojas-martinez A, et al (2009) The role of seed dispersers in the population dynamics of the columnar cactus Neobuxbaumia tetetzo. Ecology 83:2617–2629

Herrera JM, de Sá Teixeira I, Rodríguez-Pérez J, Mira A (2016) Landscape structure shapes carnivore-mediated seed dispersal kernels. Landsc Ecol 31:731–743 . doi: 10.1007/s10980-015-0283-4

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol Syst 13:201–228 . doi: 10.1146/annurev.es.13.110182.001221

Jerina K (2012) Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. J Mammal 93:1139–1148 . doi: 10.1644/11-MAMM-A-136.1

Jones JD, Kauffman MJ, Monteith KL, et al (2014) Supplemental feeding alters migration of a temperate ungulate. Ecol Appl 24:1769–1779 . doi: 10.1890/13-2092.1

Jordano P, Forget PM, Lambert JE, et al (2011) Frugivores and seed dispersal: Mechanisms and consequences for biodiversity of a key ecological interaction. In: Biology Letters.

The Royal Society, pp 321–323

Karl BJ, Clout MN (1987) An improved radio transmitter harness with a weak link to prevent snagging. J F Ornithol 58:73–77 . doi: 10.2307/4513194

Kelly D, Ladley JJ, Robertson AW, et al (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit- dispersal in New Zealand. N Z J Ecol 34:66–85

Laurance SGW, Stouffer PC, Laurance WF (2004) Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. Conserv Biol 18:1099–1109 . doi: 10.1111/j.1523-1739.2004.00268.x

Levine JM, Murrell DJ (2003) The Community-Level Consequences of Seed Dispersal Patterns. Annu Rev Ecol Evol Syst 34:549–574 . doi: 10.1146/annurev.ecolsys.34.011802.132400

McConkey KR, O'Farrill G (2016) Loss of seed dispersal before the loss of seed dispersers. Biol. Conserv. 201:38–49

Miskelly C, Beauchamp T (2004) Weka, a conservation dilemma. In: Restoring Kapiti: Nature's Second Chance. pp 81–88

Moore L, Edgar B (1970) Flora of New Zealand, Vol. II. Government Printer, Wellington, New Zealand

Morante-Filho JC, Faria D, Mariano-Neto E, Rhodes J (2015) Birds in anthropogenic landscapes: The responses of ecological groups to forest loss in the Brazilian Atlantic forest. PLoS One 10:e0128923 . doi: 10.1371/journal.pone.0128923

Morris G, Conner LM (2017) Assessment of accuracy, fix success rate, and use of estimated horizontal position error (EHPE) to filter inaccurate data collected by a common commercially available GPS logger. PLoS One 12:e0189020 . doi: 10.1371/journal.pone.0189020

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol Evol 15 278-285 15:278–285 . doi: 10.1016/S0169-5347(00)01874-7

Nathan R, Perry G, Cronin JT, et al (2003) Methods for estimating long-distance dispersal. In: Oikos. Wiley/Blackwell (10.1111), pp 261–273

O'Connor S-J (2006) Modelling seed dispersal by tūī. University of Canterbury

Prange S, Gehrt SD, Wiggers EP (2004) Influences of Anthropogenic Resources on Raccoon (Procyon lotor) Movements and Spatial Distribution. J Mammal 85:483–490 . doi:

10.1644/1383946

Robertson HA, Heather BD (1999) The field guide to the birds of New Zealand. Penguin Books, Auckland, New Zealand

Sawyer H, Kauffman MJ, Middleton AD, et al (2013) A framework for understanding semi-permeable barrier effects on migratory ungulates. J Appl Ecol 50:68–78 . doi: 10.1111/1365-2664.12013

Sengupta A, McConkey KR, Radhakrishna S (2015) Primates, provisioning and plants: Impacts of human cultural behaviours on primateecological functions. PLoS One 10:e0140961 . doi: 10.1371/journal.pone.0140961

Steadman DW (2006) Extinction and biogeography of tropical Pacific birds. University of Chicago Press, Chicago

Tucker MA, Böhning-Gaese K, Fagan WF, et al (2018) Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science (80-) 359:466–469 . doi: 10.1126/science.aam9712

Uriarte M, Anciaes M, Da Silva MTB, et al (2011) Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. Ecology 92:924–937 . doi: 10.1890/10-0709.1

Wandrag EM, Dunham AE, Duncan RP, Rogers HS (2017) Seed dispersal increases local species richness and reduces spatial turnover of tropical tree seedlings. Proc Natl Acad Sci 114:201709584 . doi: 10.1073/pnas.1709584114

Watts J (2013) Reintroducing Buff Weka (Gallirallus australis hectori) to an Unfenced Mainland Island. University of Otago

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168 . doi: 10.2307/1938423

Wotton DM, Kelly D (2012) Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. J Biogeogr 39:1973–1983 . doi: 10.1111/jbi.12000

7

Discussion

Silvereye consuming Schefflera digitata fruits. Credit: Dave Kelly

In this thesis, I aimed to assess the impact of avian declines and extinctions on seed dispersal in New Zealand. In Chapter 1, I identified several 'pinch points' for seed dispersal that may have occurred with the irrevocable alteration of New Zealand's frugivore community following human arrival. These pinch points were the loss of the moa and their potential interactions with large seeds, whether the decline of kererū was jeopardising the dispersal of large seeds, and the relative importance of flightless birds for seed dispersal in New Zealand (using the weka as a case study). By examining these potential lost interactions, I have elucidated the relative contributions of several New Zealand bird species for seed dispersal, and given insights into how robust New Zealand's seed dispersal networks are to species loss.

7.1 Does New Zealand have a 'dispersal gap' for large seeds?

Many island frugivore communities have suffered considerable losses since human arrival, often resulting in a 'downsizing' of the frugivore community due to the disproportionate vulnerability of large-bodied species to extinction (Heinen et al. 2018). As I demonstrated in Chapter 1, New Zealand is no exception to this trend, with our avian frugivore guild experiencing extinctions (in the case of the moa), range contractions (in the case of weka and kōkako), and general declines (in the case of kererū). Using Heinen et al.'s (2018) calculation method, these extinctions have corresponded to a 96% decline in the mean weight of the frugivore community since human arrival (see Chapter 1; Introduction to seed dispersal). The loss of large frugivores in particular can potentially create 'gaps' in the dispersal of large seeds, as large frugivores often have obligate relationships with these seeds (e.g. Kitamura et al. 2002). For this reason, most of the seed dispersal research in New Zealand has focused on large seeded species that are potentially more likely to suffer from dispersal failure (e.g. Clout and Hay 1989; Kelly et al. 2010; Wotton and Kelly 2012; Silberbauer 2013; Pegman et al. 2017).

However, evidence is mounting that New Zealand's large-seeded species are no more at risk of dispersal failure than small-seeded species. New Zealand's prehuman ecosystems were dominated by its largest birds, the moa. If these avian megafauna

were important dispersers of large seeds, then their subsequent extinction could have impaired the dispersal of large seeds. However, I have demonstrated that moa only dispersed seeds smaller than 3.3 mm (Chapter 3), and actually destroyed most seeds they consumed, so the loss of moa has not created a gap in the dispersal of large seeds. Therefore, if we reclassify the nine species of moa as seed predators rather than frugivores and consequently remove them from the analysis of the pre- and post-human frugivore community weights (Chapter 1), we find that the New Zealand frugivore community has actually only experienced a small downsizing since human arrival – from 0.78 kg, to 0.7 kg (a 10% decrease). This reveals the risks of using broad calculations based on inferences about extinct species to demonstrate loss of ecological function.

Furthermore, it appears that poor dispersal service does not correlate with seed size in the New Zealand flora. In Chapter 2, I demonstrated that several large-seeded tree species are receiving adequate seed dispersal services (with the exception of hīnau). Similarly, Macfarlane et al. (2015) found that large seeds were no more likely to be undispersed than small seeds in a forest fragment near Kaikoura with only bellbirds, silvereyes, blackbirds, and starlings present. This finding is supported by Kelly et al. (2010), who showed that the variance in both seed size and bird gape size enables most species to be dispersed by more species than just kererū. Although Wotton and Kelly (2012) demonstrated that the consequences of non-dispersal for two of New Zealand's largest species (taraire and karaka) would be fairly large, there was only quite limited information on whether the dispersal of these two species was actually failing.

On the whole, it therefore appears that New Zealand's large seeds are currently not suffering systematically worse dispersal than small seeds. This finding is in direct contrast to overseas studies, which have overwhelmingly demonstrated that large-seeded species are particularly susceptible to the loss of large frugivores (e.g. Meehan et al. 2002; Moran et al. 2009; Vanthomme et al. 2010; Kurten 2013; Doughty et al. 2016). For example, a review by Kurten (2013) confirmed that larger seeded species consistently experience reduced primary seed dispersal and increased seedling aggregation around parent trees, as a result of defaunation. Similarly, Vanthomme et

al. (2010) demonstrated that the diversity of seedlings at a site in Central Africa was reduced at heavily hunted sites, especially for large seeded species dispersed by large game animals. The New Zealand situation differs from these overseas examples because a) New Zealand still retains its largest bodied frugivores, the kea, weka, and kererū, b) no native plant species have seeds which are beyond the gape size of these three species, partly because compared to their overseas counterparts, New Zealand fruits are small (Lord 2002) and kererū are large (Kelly et al. 2010), and c) kererū at least still remain reasonably widespread across New Zealand, even though they have declined from their prehuman abundances (Lyver et al. 2008). Therefore, while levels of dispersal are very likely lower than they were in prehuman times, this does not seem to disproportionately affect large-seeded species.

So which seeds are experiencing poor dispersal in contemporary New Zealand? Kelly et al. (2010) reviewed the fruit removal rates and dispersal levels published for ten species and concluded that only *Pittosporum crassifolium* (a small-seeded species) had levels of dispersal that could be quantified as 'poor' (only 20% of seed dispersed on the mainland, compared to 94% in a bird sanctuary). Since then, several more studies have highlighted species with poor dispersal service. Wyman (2013) recorded poor dispersal for *Coprosma areolata* within a Canterbury forest fragment, while this thesis has shown that hīnau suffers from impaired fruit removal rates on the New Zealand mainland. Finally, Macfarlane et al. (2015) recorded no dispersal of *Ripogonum scandens, Leucopogon fasciculatus, Cordyline australis, Myrsine australis, Corokia cotoneaster, Myoporum laetum, Coprosma grandifolia,* and *Hedycarya arborea* at Kowhai Bush, in Kaikoura. However, they noted that some of those species were uncommon at their site, so that the failure to detect dispersal could be a sampling problem.

Drivers of poor dispersal service could include reduced frugivore numbers, local or total extinction of key dispersers (as is the case for hīnau on much of the New Zealand mainland where weka are absent), or simply low density of the plant at the site. Generally, there is a positive correlation between dispersal service and bird density, with plants receiving better dispersal service at high-bird-density sites such as sanctuaries and islands (Iles 2012; Wyman 2013; Carpenter et al. 2018). Wyman (2013)

suggested that when bird density is reduced, low-reward plant species are at most risk of dispersal failure. Therefore, there is a possibility that the species recorded with poor dispersal rates may have less attractive fruits that suffer when bird densities are low. I recommend that future studies on seed dispersal in New Zealand include comparisons between mainland sites and bird sanctuary sites. Such studies will help to disentangle drivers of poor dispersal, and enhance understanding of baseline dispersal levels. In addition, future studies on seed dispersal quantity could attempt to align their methodology with that used by the national seed rain network (seed traps beneath parent trees; see Chapter 2), in order to capitalise on a large existing dataset and enable comparisons across multiple sites and years.

7.2 Which dispersers matter? The sociology of seed dispersal

Understanding how avian seed dispersal fares with 'the wreckage of an avifauna' (Kelly et al. 2010) requires knowing the relative contributions of each bird species to seed dispersal. The contribution of each species can be considered as an interaction between the seed dispersal quantity (e.g. fruit removal rate) and seed dispersal quality (e.g. treatment of seeds in gut, or dispersal distance) they provide (Schupp et al. 2010).

In New Zealand, several studies have assessed levels of dispersal quantity by various frugivorous birds at the community level (O'Donnell and Dilks 1994; Burns 2012; García et al. 2014; MacFarlane et al. 2016). A review by Kelly et al. (2006) concluded that bellbirds, tūī, kererū, and silvereyes conducted 84% of all feeding observations on native fruits, while Burns (2012) and Garcia et al. (2014) argued that introduced frugivores also conducted important seed dispersal services. Introduced birds are probably important seed dispersers in or near urban habitats, where their absolute and relative abundances are high, compared to remote environs where they are far less common (MacFarlane et al. 2016). Although these studies give valuable insights into the relative importance of extant birds across specific sites, they fail to record lost interactions between plants and locally (or globally) extinct species. For example, none of these community level studies included weka or kōkako, so their seed dispersal contributions relative to other species were still unknown (but see Chapter 4). This is a

limitation that has also been acknowledged by Anderson et al. (2016) for bird pollination studies, which frequently assess floral visitations without reporting the historical community of pollinators that would have coexisted with the plant species but may now be absent.

The quality of seed dispersal provided by birds is an essential part of assessing their relative contributions, but studies on seed dispersal quality provided by New Zealand birds are rare. Ladley and Kelly (1996) measured fruit removal rate for four native mistletoes and mistletoe seeds per dropping for various native birds (dispersal quantity) and germination of bird-passed seeds (dispersal quantity). Kelly et al. (2010) extended this to test the germination effects of bird gut passage on a wide range of native tree species. Wotton (2007) assessed how kererū gut passage affected germination of seeds, and created a mechanistic model to estimate kererū dispersal distances (Wotton and Kelly 2012). O'Connor (2006) also created a mechanistic model to estimate seed dispersal distances provided by tūī. Young (2012) tested the effect of kea consumption on the germination of several species of alpine plants, and assessed the suitability of microsites for germination (Young and Kelly 2018). Wyman and Kelly (2017) compared how gut passage through possums, silvereyes, bellbirds, blackbirds, silvereyes and thrushes affected germination of *Coprosma robusta* seeds and found that only possums had a different effect (a reduction relative to hand-cleaned seeds). Finally, I have estimated the seed dispersal distances provided by weka to miro and hīnau (Chapter 6). Germination experiments with weka-consumed seeds would be a valuable next step in revealing the seed dispersal capabilities of weka. However, the quality of dispersal provided by most New Zealand birds is still unknown, even for widespread and common birds like the silvereye and bellbird. Studies which assess an aspect of dispersal quality (e.g. percentage of seeds dispersed away from parent canopies) across the entire frugivore community would be extremely valuable, although these studies are still rare even overseas (but see González-Castro et al. 2015; Nogales et al. 2017; Fricke et al. 2018a; Rehm et al. 2019).

The lack of data on the seed dispersal quality and quantity provided by many New Zealand avian frugivores can result in incorrect assumptions being made about each species' relative importance. For example, kererū became increasingly lauded as a

keystone frugivore throughout the late 20th century (McEwan 1978), culminating in Clout and Hay's (1989) overly broad assessment that they were "virtually the sole disperser" for eleven large-seeded plant species (an idea repeated by Lee et al. 1991; Clout and Tilley 1992; Webb and Kelly 1993; Southward et al. 2002; and Emeny et al. 2009, among others). Kelly et al. (2010) demonstrated that in reality, kererū are probably the primary disperser for only six plant species (and "virtually the sole disperser" for only one, taraire), and that mid-sized birds such as tūī and bellbirds are also important for the dispersal of large seeds. Similarly, moa were frequently speculated to be important dispersers of large seeds in New Zealand's prehuman ecosystems (Clout and Hay 1989; Lee et al. 1991; Kelly et al. 2010), but my thesis has demonstrated that they actually only dispersed small seeds and (especially for large fruits) functioned more as seed predators. Finally, the humble weka has been grossly overlooked in the seed dispersal literature, with Lee et al. (1991) recording them as "primarily omnivorous or insectivorous, and their frugivory is mostly occasional", Clout and Hay (1989) dismissing them as they "have restricted distributions so are not major seed dispersers", and Lord et al. (2002) briefly mentioning them as "minor frugivores". However, I have demonstrated that weka are key dispersers for hīnau (Chapter 4) and probably several other plant species, with extremely long seed retention times (Chapter 5) and good quality seed dispersal (Chapter 6). Those long retention times could also make weka important long-distance dispersers even for plant species where weka eat a minority of fruits, equivalent to the carnivorous mammals which ate few *Prunus mahaleb*, but moved most seeds they ate a long distance (Jordano et al. 2007).

The importance of kererū and moa as seed dispersers has therefore arguably been overstated in the literature, while weka have been underappreciated. What drives these incorrect assumptions? I propose several hypotheses. The first is that omnivorous species are perhaps considered a seed dispersal sideshow, compared to species which are exclusively or predominantly frugivorous. This is presumably (and not unreasonably) based on an intuitive sense of dispersal quantity. For example, many of the dismissive comments about weka in the seed dispersal literature refer to the fact that they are not exclusively frugivorous. This ignores the fact that diet is just one facet of dispersal service, and relates solely to dispersal quantity rather than

dispersal quality. Even within that, fruit being a low percentage of the diet of the animal corresponds only loosely to a low fraction of the fruit crop being consumed by that animal (the latter being the definition of dispersal quantity), depending among many other factors on the abundance of dispersers per hectare and plants per hectare. In addition, even partially frugivorous species can still provide good dispersal quantity if they concentrate on fruits when these are seasonally available (as is the case for weka). For example, in Spain three species of carnivorous mammals (foxes, badgers, and stone martens) are seasonally important dispersers and provide excellent long-distance dispersal, despite fruit being only a small component of their overall diet (Herrera 1995; Jordano et al. 2007). These findings demonstrate that species which are not predominantly frugivorous should not be discounted as important seed dispersers.

Secondly, ecologists may tend to overstate the importance of extinct species, such as moa, for two reasons: these are the species that are generally most data deficient, and perhaps we are more likely to worry about an interaction that is already lost. For example, the possible role of extinct megafauna as important seed dispersers has been a popular area of research (e.g. Guimarães et al. 2008; Galetti et al. 2017; van Zonneveld et al. 2018; Pires et al. 2018). Lastly, the ecological novelty or uniqueness of a species may make it more salient and mean its importance is more likely to be overstated. For example, the very large size of some of the moa species has always led to extensive speculations about their putative qualitatively unique influences on New Zealand ecosystems. Weka, on the other hand, are one of several rail species still present in New Zealand.

When data are lacking, assumptions are understandable. However, I have challenged these assumptions by showing that omnivorous birds can also contribute important dispersal services, and that the extinction of large birds does not necessarily also entail lost interactions with large seeds. Based on my findings, I would recommend ecologists clearly review the existing data when assessing whether a species contributes important seed dispersal services or not, rather than making assumptions based on biased ideas. These perceptions can stand in the way of new research being conducted that more clearly outlines various species' contributions.

7.3 The importance of (cryptic) functional diversity

Islands are often characterized by low species diversity, and anthropogenic changes have frequently caused extinctions that further diminish this diversity (Whittaker and Fernández-Palacios 2007; Heinen et al. 2018). This low species diversity can result in simplified seed dispersal networks with low redundancy, where few mutualistic partners perform the same role (Kaiser-Bunbury et al. 2010). For example, flying foxes in Tonga perform seed dispersal services that are not compensated by other available seed dispersers (birds, crabs, and rats) when flying foxes are functionally extinct – a vulnerable situation (McConkey and Drake 2015).

Initially, New Zealand's seed dispersal networks may appear to include a reasonable amount of redundancy, being predominantly composed of frugivorous birds with some dietary overlap (O'Donnell and Dilks 1994; Kelly et al. 2010), so that with the exception of the very largest seeded tree species most plant species are dispersed by more than one mutualistic partner (Wyman 2013; García et al. 2014). However, I argue that like other island systems (e.g. Galapagos, Rumeu et al. 2017), New Zealand seed dispersal networks may feature more functional diversity and therefore less redundancy than initially meets the eye. I have demonstrated that our largest seed dispersers, the moa, functioned similarly to large ungulate herbivores overseas (Chen and Moles 2015), dispersing small seeded herbaceous plants and destroying large seeds. This role is not compensated for by any extant species, with the possible important but untested exception of introduced ungulates (but see Young 2012). Weka arguably influence seed dispersal kernels in a similar way to carnivorous mammals in Spain, where Jordano et al. (2007) demonstrated that foxes, badgers, and stone martens disperse *Prunus maleb* seeds much further distances than small passerines. Like these carnivorous mammals, weka are not exclusively frugivorous but still consume fruit and provide important dispersal services for some species. In addition, the long seed retention times of weka (means of 39 and 125 hours for miro and hīnau) are more like those of mammals rather than birds, as mammals of a comparative size to weka have mean retention times between 10 and 100 hours (Fritz et al. 2012). Tūī, on the other hand, have very short seed retention times (33-40 minutes) but are highly mobile,

dispersing *Coprosma* seeds over 200 m (O'Connor 2006). These results suggest that weka, tūī, and other small passerines may all contribute to different aspects of seed dispersal shadows, much as Rehm et al. (2019) found for five bird species in Saipan. Therefore, the dispersal services of many New Zealand bird species are probably complementary rather than redundant – a theme that is being increasingly observed in seed dispersal networks (Fricke et al. 2018b). Further study would probably reveal other distinctive roles played by various bird species, and this would be an interesting avenue of future research.

New Zealand's seed disperser guild therefore demonstrates a kind of 'cryptic functional diversity', where even though the frugivore community is dominated by birds, these birds are performing quite different seed dispersal services. The question is, does this diversity affect outcomes for plants in a meaningful way (i.e. growth, survival, reproduction)? In some cases, the answer is yes. For example, the effect of gut passage on seed germination is a key functional outcome of seed dispersal interactions. While the most important frugivorous birds in New Zealand (Kelly et al. 2006) do not exhibit functional diversity in their effect on germination (Ladley and Kelly 1996; Wyman and Kelly 2017), my research has shown that hīnau seeds that have been mildly abraded increase their germination by 27.5 percentage points compared to hand cleaned seeds – a 2.3 fold increase (Chapter 3; Appendix 3.6.4). These results suggest that the mild abrasion conferred by the grit-filled gizzards of weka may confer benefits to some plant species that birds with soft digestive tracts and short seed retention times do not provide. In addition, differences in the proportion of seeds that are dispersed beneath parent canopies by different birds are also likely to affect functional outcomes for plants, especially where Janzen-Connell effects exist (e.g. Wotton and Kelly 2012). For example, Cowan and Waddington (1991) noted that hīnau seedling survival in the Orongorongo Valley appeared higher away from parent trees – so the difference between kererū dispersing ~30% of seeds beneath the canopy compared to 4% of seeds dispersed beneath the canopy by weka could translate to large differences in recruitment for hīnau. Furthermore, some New Zealand studies have recorded plant species that were only dispersed by one bird species at certain sites, despite those fruits being within the gape size of other frugivorous birds that

were present at the site (Wyman 2013; MacFarlane et al. 2016). Where these obligate relationships exist, then the bird species servicing those plants are undeniably important. Studies overseas are also demonstrating that functional diversity in frugivore communities is probably very important for the ongoing maintenance of plant communities. For example, Garcia and Martinez (2012) found that the quality of seed dispersal (in this case, seed deposition in open microsites) was mostly dependent on frugivore richness. Similarly, Rumeu et al. (2017) demonstrated that the richness of the Galapagos seed dispersal community was a powerful predictor of the number of plant species receiving adequate dispersal, especially when the overall abundance of dispersers decreased.

Therefore, New Zealand's seed dispersal networks are probably less resistant to species loss than they initially appear, as the species richness and functional diversity of the frugivore community is an important driver of seed dispersal processes. However, simply identifying every bird species as providing critical and unique dispersal services is probably not true, and even if it was, would not be realistic for conservation prioritization efforts. There is a need to capture the key sources of functional variation within our avian frugivore guild and develop techniques that allow generalisation so that important components can be identified and conserved (Fricke et al. 2018a). Fricke et al. (2018a) attempted this in Saipan, by conducting experiments to assess the impact of the five extant frugivorous birds' gut passage on germination success. Based on their results, they suggested that they could have functionally grouped the five species simply as 'birds', because with the exception of one species which functioned more as a seed predator, all other species had the same effect on plant germination. My own findings suggest that lumping New Zealand's frugivorous birds into one functional group would ignore the meaningful functional diversity that exists within the coterie. Dennis and Westcott (2006) outlined a classification system for functional groups of frugivores in tropical forests, which allowed them to separate 65 Australian vertebrate seed dispersers into 15 functional groups based on the type of dispersal each species provides and the fruit types it disperses. Using Dennis and Westcott's (2006) classification system on extant and endemic New Zealand avian frugivores separates most of the birds into distinct functional groups, which seems

overly complex (Table 1). In addition, some of the species could debatably be allocated instead to another functional group, which negates the value of the whole exercise. However, as New Zealand's avian frugivore community is relatively depauperate compared to tropical systems I think that simply identifying the important extant functional groups taxonomically as pigeons, passerines, Dinornithiformes, and rails would probably capture most of the important functional diversity within New Zealand's avian frugivores. This grouping would allow key functional groups of dispersers to be maintained, and ensure the ongoing maintenance of New Zealand's seed dispersal networks.

Table 7.1. *Native New Zealand birds grouped by seed dispersal function following Dennis and Westcott's (2006) classification system.*

Dennis & Westcott Functional Group	*Possible New Zealand species*
Wide-ranging frugivore	Kōkako
Small within-forest frugivore	Tīeke (2 species)
Wide-ranging large fruit	Tūī, Kererū
Mega terrestrial frugivores	Weka
Digestive predators	Moa (9 species)
Throughout-landscape frugivores	Silvereyes, Bellbirds

In conclusion, this thesis has revealed some surprising findings regarding the roles played by both extinct and extant bird species for seed dispersal in New Zealand, that challenge previous assumptions. I argue that the lesson to be learned from this is the importance of fully understanding the underlying natural history. While statistical modelling and network analysis become ever more advanced and sophisticated, these approaches are only as good as the data they use. A basic understanding of what each animal species contributes in terms of plant species consumed and whether they pass seeds intact, while not glamorous, is critical to making accurate predictions about how these interactions will fare in the face of species loss. As an example of this, O'Donnell

and Dilks' (1994) paper with quantitative feeding observations of forest birds in South Westland, while not 'high impact' by many of today's metrics, is an invaluable resource for anyone researching New Zealand's seed dispersal networks. With this in mind, and based on the data we do have, it appears that New Zealand seed dispersal interactions are probably working adequately on the whole, but there are still considerable gaps in our knowledge which need to be filled before we can state this with confidence.

7.4 References

Anderson S, Kelly D, Robertson A, Ladley J (2016) Pollination by birds: a functional evaluation. In: Sekercioglu C, Wenny D, Whelan C (eds) Why birds matter: avian ecological functions and ecosystem services. University of Chicago Press, Chicago

Burns KC (2012) Are introduced birds unimportant mutualists? A case study of frugivory in European blackbirds (Turdus merula). N Z J Ecol 36:171–176 . doi: http://dx.doi.org/10.1016/j.ijforecast.2011.04.001

Carpenter JK, Kelly D, Clout MN, et al (2017) Trends in the detections of a large frugivore (Hemiphaga novaeseelandiae) and fleshy-fruited seed dispersal over three decades. N Z J Ecol 41:41–46 . doi: 10.20417/nzjecol.41.17

Carpenter JK, Kelly D, Moltchanova E, O'Donnell CFJ (2018) Introduction of mammalian seed predators and the loss of an endemic flightless bird impair seed dispersal of the New Zealand tree Elaeocarpus dentatus. Ecol. Evol. 1–13

Chen SC, Moles AT (2015) A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. Glob Ecol Biogeogr 24:1269–1280 . doi: 10.1111/geb.12346

Clout MN, Hay JR (1989) The importance of birds As browsers, pollinators and seed dispersers in New Zealand forests. N Z J Ecol 27–33 . doi: 10.2307/24053245

Clout MN, Tilley JAV (1992) Germination of miro (Prumnopitys ferruginea) seeds after consumption by New Zealand pigeons (Hemiphaga novaeseelandiae). New Zeal J Bot 30:25–28 . doi: 10.1080/0028825X.1992.10412882

Cowan PE, Waddington DC (1991) Litterfall under hinau, Elaeocarpus dentatus, in lowland podocarp/mixed hardwood forest, and the impact of brushtail possums, Trichosurus vulpecula. New Zeal J Bot 29:385–394 . doi: 10.1080/0028825X.1991.10415491

Dennis AJ, Westcott DA (2006) Reducing complexity when studying seed dispersal at community scales: A functional classification of vertebrate seed dispersers in tropical forests. Oecologia 149:620–634 . doi: 10.1007/s00442-006-0475-3

Doughty CE, Wolf A, Morueta-Holme N, et al (2016) Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. Ecography (Cop) 39:194–203 . doi: 10.1111/ecog.01587

Emeny MT, Powlesland RG, Henderson IM, Fordham RA (2009) Feeding ecology of kereru (Hemiphaga novaeseelandiae) in podocarp-hardwood forest, Whirinaki Forest Park, New Zealand. N Z J Ecol 33:114–124

Fricke EC, Bender J, Rehm EM, Rogers HS (2018a) Functional outcomes of mutualistic network interactions: a community-scale study of frugivore gut passage on germination. J Ecol 1–11 . doi: 10.1111/1365-2745.13108

Fricke EC, Tewksbury JJ, Rogers HS (2018b) Defaunation leads to interaction deficits, not interaction compensation, in an island seed dispersal network. Glob Chang Biol 24:e190–e200 . doi: 10.1111/gcb.13832

Fritz J, Hammer S, Hebel C, et al (2012) Retention of solutes and different-sized particles in the digestive tract of the ostrich (Struthio camelus massaicus), and a comparison with mammals and reptiles. Comp Biochem Physiol - A Mol Integr Physiol 163:56–65 . doi: 10.1016/j.cbpa.2012.05.184

Galetti M, Mole M, Jordano P, et al (2017) Ecological and evolutionary legacy of megafauna extinctions. Biol Rev. doi: 10.1111/brv.12374

Garcia D, Martinez D (2012) Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. Proc R Soc B Biol Sci 22:13–18 . doi: 10.1098/rspb.2012.0175

García D, Martínez D, Stouffer DB, Tylianakis JM (2014) Exotic birds increase generalization and compensate for native bird decline in plant-frugivore assemblages. J Anim Ecol 83:1441–1450 . doi: 10.1111/1365-2656.12237

González-Castro A, Calviño-Cancela M, Nogales M (2015) Comparing seed dispersal effectiveness by frugivores at the community level. Ecology 96:808–818 . doi: 10.1890/14-0655.1

Guimarães PR, Galetti M, Jordano P (2008) Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. PLoS One 3:e1745 . doi: 10.1371/journal.pone.0001745

Heinen JH, van Loon EE, Hansen DM, Kissling WD (2018) Extinction-driven changes in frugivore communities on oceanic islands. Ecography (Cop) 41:1245–1255 . doi: 10.1111/ecog.03462

Herrera CM (1995) Dispersal systems in the Mediterranean: Ecological, Evolutionary, and Historical Determinants. Annu Rev Ecol Syst 26:705–727 . doi: 10.1146/annurev.es.26.110195.003421

Iles JM (2012) Is Maungatautari restoring bird pollination and seed dispersal services? University of Canterbury

Jordano P, Garcia C, Godoy JA, Garcia-Castano JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. Proc Natl Acad Sci 104:3278–3282 .

doi: 10.1073/pnas.0606793104

Kaiser-Bunbury CN, Traveset A, Hansen DM (2010) Conservation and restoration of plant-animal mutualisms on oceanic islands. Perspect. Plant Ecol. Evol. Syst. 12:131–143

Kelly D, Ladley JJ, Robertson AW, et al (2010) Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit- dispersal in New Zealand. N Z J Ecol 34:66–85

Kelly D, Robertson AW, Ladley JJ, et al (2006) Relative (un)importance of introduced animals as pollinators and dispersers of native plants. In: Biological Invasions in New Zealand. pp 227–245

Kitamura S, Yumoto T, Poonswad P, et al (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. Oecologia 133:559–572 . doi: 10.1007/s00442-002-1073-7

Kurten EL (2013) Cascading effects of contemporaneous defaunation on tropical forest communities. Biol. Conserv. 163:22–32

Ladley JJ, Kelly D (1996) Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): Dependence on birds. N Z J Ecol 20:69–79 . doi: 10.2307/24053735

Lee WG, Clout MN, Robertson HA, Bastow Wilson J (1991) Avian dispersers and fleshy fruits in New Zealand. Proc Int Orn Congr XX 1617–1623

Lord J (2002) Have frugivores influenced the evolution of fruit traits in New Zealand? In: DJ L, WR S, M G (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, WallingfoRd, UK, pp 55–68

Lyver PO, Taputu TM, Kutia ST, Tahi B (2008) Tūhoe Tuawhenua mātauranga of kererū (Hemiphaga novaseelandiae novaseelandiae) in Te Urewera. N Z J Ecol 32:7–17 . doi: 10.2307/24058096

MacFarlane AET, Kelly D, Briskie J V (2016) Introduced blackbirds and song thrushes: Useful substitutes for lost mid-sized native frugivores, or weed vectors? N Z J Ecol 40: . doi: 10.20417/nzjecol.40.9

McConkey KR, Drake DR (2015) Low redundancy in seed dispersal within an island frugivore community. AoB Plants 7:plv088 . doi: 10.1093/aobpla/plv088

McEwan WM (1978) The food of the New Zealand pigeon (Hemiphaga novaeseelandiae novaeseelandiae). N Z J Ecol 1:99–108 . doi: 10.1002/jid

Meehan HJ, McConkey KR, Drake DR (2002) Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. J Biogeogr 29:695–712 . doi:

10.1046/j.1365-2699.2002.00718.x

Moran C, Catterall CP, Kanowski J (2009) Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. Biol Conserv 142:541–552 . doi: 10.1016/j.biocon.2008.11.006

Nogales M, González-Castro A, Rumeu B, et al (2017) Contribution by vertebrates to seed dispersal effectiveness in the Galápagos Islands: a community-wide approach. Ecology 98:2049–2058 . doi: 10.1002/ecy.1816

O'Connor S-J (2006) Modelling seed dispersal by tui. University of Canterbury

O'Donnell CFJ, Dilks PJ (1994) Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. N Z J Ecol 18:87–107 . doi: 10.1093/iis/etq042

Pegman APMcK, Perry GLW, Clout MN (2017) Size-based fruit selection by a keystone avian frugivore and effects on seed viability. New Zeal J Bot 55:118–133 . doi: 10.1080/0028825X.2016.1247882

Pires MM, Guimarães PR, Galetti M, Jordano P (2018) Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. Ecography (Cop) 41:153–163 . doi: 10.1111/ecog.03163

Rehm E, Fricke E, Bender J, et al (2019) Animal movement drives variation in seed dispersal distance in a plant–animal network. Proc R Soc B Biol Sci 286:20182007 . doi: 10.1098/rspb.2018.2007

Rumeu B, Devoto M, Traveset A, et al (2017) Predicting the consequences of disperser extinction: richness matters the most when abundance is low. Funct Ecol 31:1910–1920 . doi: 10.1111/1365-2435.12897

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: A conceptual review. New Phytol. 188:333–353

Silberbauer RB (2013) Benefits of seed dispersal for escaping seed predation and examining the life history, host suitability/preference and impact of the polyphagous obligate seed predator Cryptaspasma querula. Massey University, New Zealand

Southward RC, Fountain DW, Gao R, et al (2002) Biology, structure, and germination characteristics of seeds of puriri Vitex lucens (Verbenaceae). New Zeal J Bot 40:427–435 . doi: 10.1080/0028825X.2002.9512804

van Zonneveld M, Larranaga N, Blonder B, et al (2018) Human diets drive range expansion of megafauna-dispersed fruit species. Proc Natl Acad Sci 201718045 . doi: 10.1073/pnas.1718045115

Vanthomme H, Bellé B, Forget PM (2010) Bushmeat hunting alters recruitment of large-seeded plant species in Central Africa. Biotropica 42:672–679 . doi: 10.1111/j.1744-7429.2010.00630.x

Webb CJ, Kelly D (1993) The reproductive biology of the New Zealand flora. Trends Ecol. Evol. 8:442–447

Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: Ecology, evolution, and conservation. Oxford University Press

Wotton DM (2007) Consequences of dispersal failure: kereru and large seeds in New Zealand. University of Canterbury

Wotton DM, Kelly D (2012) Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. J Biogeogr 39:1973–1983 . doi: 10.1111/jbi.12000

Wyman TE (2013) Consequences of reduced bird densities for seed dispersal. University of Canterbury

Wyman TE, Kelly D (2017) Quantifying seed dispersal by birds and possums in a lowland New Zealand forest. N Z J Ecol 41:47–55 . doi: 10.20417/nzjecol.41.4

Young LM (2012) Seed dispersal mutualisms and plant regeneration in New Zealand alpine ecosystems. University of Canterbury

Young LM, Kelly D (2018) Effects of seed dispersal and microsite features on seedling establishment in New Zealand fleshy-fruited perennial mountain plants. Austral Ecol 43:775–785 . doi: 10.1111/aec.12620

Young LM, Kelly D, Nelson XJ (2012) Alpine flora may depend on declining frugivorous parrot for seed dispersal. Biol Conserv 147:133–142 . doi: 10.1016/j.biocon.2011.12.023